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PHYLOGENY AND ZOOGEOGRAPHY OF *LAEMONEMA* AND *GUTTIGADUS* (PISCES; GADIFORMES; MORIDAE)

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ABSTRACT

The systematics of the "Laemonema" subgroup were examined and resulted in recognition of two genera, *Laemonema* with 12 species, and *Guttigadus* with eight species (including two of uncertain status). Two new species of *Laemonema* are described from the Indian Ocean and western Atlantic. Juvenile (*Svetovidovia*) stages are known for *L. barbatulum, L. melanurum, L. verecundum* and the new western Atlantic form. All have an unpigmented posterior trunk whereas the known juvenile stages of *Guttigadus* have numerous vertical bars not found in *Laemonema*. *Laemonema* and *Guttigadus* are largely allopatric over similar depth ranges. *Laemonema* is primarily tropical ranging from 60° N to 40° S in 50-1900 m, and *Guttigadus* is primarily in the Southern Ocean from 25° - 59° S in 25-1900 m. About half of all *Laemonema* are oceanic, associated with islands and seamounts, and half have continental affinities. Two terminal species pairs of *Laemonema* are allopatric, each showing east-west segregation involving an oceanic-continental pair. Two dwarfed, pelagic, paedomorphic species in the North Pacific, *L. verecundum* and *G. nana*, have been classified as monotypic genera. We place *L. verecundum* as the sister to *L. longipes* and *G. nana* as the earliest clade in *Guttigadus*, but believe that further study of paedomorphosis in the group is warranted.

According to Cohen et al. (1990), half of the known species of gadiform fish live in deep water, are mainly small, some are apparently rare, and many have taxonomic problems. One family meeting all of these characteristics is Moridae, recognized by Svetovidov (1948) and separated from Gadidae, based on features of the olfactory nerves, interorbital septum, neurocranium, and especially, an otophysic connection between the swimbladder and the auditory capsules (Paulin, 1988). Cohen et al. (1990) included 19 genera and 91 species in Moridae but indicated that the list is not complete because of many taxonomic problems.

Otolith morphology has been the primary data source for higher level morid classifications (Karrer, 1971; Paulin, 1983, 1989). Three groups established by Karrer (1971) are usually recognized. For example, Paulin (1989) recognized the "*Mora*" group (*Mora, Halargyreus, Lepidion,* and *Antimora*), the "*Pseudophycis*" group (*Pseudophycis, Lotella,* and *Eyorius*), and the "*Physiculus*" group. His "*Physiculus*" group had two subgroups "*Physiculus*" (*Physiculus, Gadella, Salilota* and *Tripterophycis*) and "*Laemonema*" (*Laemonema, Microlepidium, Podonematichthys,* and *Momonatira*). He treated the following genera *incertae sedis*: *Austrophycis* (possibly part of the *Pseudophycis* group), *Auchenoceros* (also possibly part of the *Pseudophycis* group, but convergent with *Laemonema*), and the fossil taxon *Actuariolum*. Several additional genera not treated by Paulin, but relevant to this study, are *Paralaemonema* Trunov, 1990 with three species considered close to *Laemonema, Guttigadus,* and two based on juveniles (*Svetovidovia* and *Laemonemodes*). *Svetovidovia*, was tentatively referred to *Laemonema* by Fahay and Markle (1984) and *Laemonemodes* synonymized by Norman (1966).

The nomenclature, definition and content of *Laemonema* are problematic. The authority for the genus name and the correct type species were confounded by almost simulta-

neous publication. In June 1862, Johnson described a new species from Madeira, *Laemonema robustum*, which he referred to Günther's genus *Laemonema*. However, it was 5 mo later that Günther described *Laemonema* based on *Phycis yarrelli* Lowe, 1838.

Several authors have suggested that *Laemonema* requires revision (Holt and Byrne, 1908a; Rass, 1954), and Karrer (1971) noted that it might be polyphyletic. Rass (1954) thought *Laemonema* naturally formed two distinct groups: a narrow-headed group with an interorbital space < 1/4 head length as well as a protruding upper jaw and chin barbel, including *L. yarrelli*, *L. robustum*, *L. barbatulum*, *L. gracillipes*, and *L. rhodochir*; and a broad-headed group with a interorbital > 1/3 head length as well as subequal jaws and a rudimentary or no barbel, including *L. latifrons* and *L. globiceps*. The lack of a revision has resulted in a number of genus-level names, usually erected for relatively distinctive forms such as *Guttigadus* Taki, 1953 for *G. nana*, *Microlepidium* Garman, 1899 for *M. verecundum*, *Podonema* Rass, 1954 for *P. longipes*, *Momonatira* Paulin, 1985 for *M. globosus*, and *Paralaemonema* Trunov, 1990 for *P. nudirostre* Trunov, 1990).

The *Laemonema* subgroup as defined by Paulin (1989), plus *Paralaemonema*, herein called *Laemonema* sensu lato, is mainly a genus of the continental slope and is distributed in almost all oceans from approximately 59° S to 60° N. Fossil evidence of *Laemonema* sensu lato comes mainly from otoliths and dates at least to the Miocene (Nolf and Steurbaut 1989). The shallowest species is *L. nana*, which lives in 25-60 m off Japan. The deepest record is 1900 m for both *L. latifrons* (IOS 51021) in the Celtic Sea (eastern North Atlantic) and *L. longipes* in the western North Pacific (Pautov 1980). The purpose of this paper is to revise the taxonomy of *Laemonema* sensu lato and provide a preliminary phylogeny and zoogeographic analysis.

Materials and Methods

All nominal species of *Laemonema* sensu lato are treated as the ingroup. At least one specimen of each recognized species was examined except for *G. nudirostre* (Trunov, 1990), *G. squamirostre* (Trunov, 1990), and *L. yuvto* Parin and Sazonov, 1990. The morids *Austrophycis marginatus* (Günther, 1878), *Lepidion eques* (Günther, 1887), *Lotella fernandeziana* Rendhal, 1921, and *Physiculus fulvus* Bean, 1884, were selected as out-groups. The selection of out-groups follows Paulin's (1989) groups but was limited by availability of specimens. Institutional abbreviations for material examined follow Leviton et al. (1985). The material examined sections include museum catalog numbers and, for new taxa, the number, standard length (mm) range, and locality.

Morphometric and meristic characters were measured according to Hubbs and Lagler (1954), Paulin (1983), and Markle and Meléndez (1988); abbreviations used are as follows. The morphometric characters were: head length (HL), snout length (SNT), barbel length (BARBEL), orbit diameter (ORB), interorbital width (INT), maxillary (UJL), predorsal length (PDL), first dorsal fin height (D1H), second dorsal fin length (D2L), preanal fin length (PAL), preanus length (PANUS), anal fin length (AL), body depth at base of first anal ray (BD-IA), postorbital length (POSTOR), prepectoral fin length (PREPECT), prepelvic fin length (PREPELVIC), pelvic fin ray length (PELVRAYL), pectoral fin ray length (PECTRAYL), first dorsal fin base length (D1BASE), pectoral fin base length (PECTBASE), maximum body depth (MAXDEPTH), minimum caudal peduncle depth (CAUDDEPTH), and body depth at anus (DEPTHANUS). Morphometric characters were not measured in specimens that were shrunk or in bad condition.

The meristic characters were: first dorsal fin rays (D1), second dorsal fin rays (D2), anal fin rays (A), pectoral fin rays (P1), pelvic fin rays (P2), precaudal vertebrae (PCV), caudal vertebrae, excluding the ural centra (CV), total vertebrae, excluding the ural centra (TV), lower gill rakers (LGR), upper gill rakers (UGR), total gill rakers (TGR), upper procurrent caudal fin rays (UPPCR), princi-

Table 1. List of abbreviations used in the Figures 4-16.

A - actinosts
AR - opercular arm of hyomandibular
B - basipterygia
C - coracoid
CJ - cartilaginous joint of pelvic girdle
CL - cleithrum
C1 - anterior chamber of swimbladder
C2 - posterior chamber of swimbladder
E - epurals
EN - elongate neck of swimbladder
E1-4 - epibranchials 1 to 4
F - foramen
F1 - first rays of the first dorsal fin
H - hypurals
IC - interarcual cartilage
IL - interarcual ligament
L - ligament, unspecified
LPB - antero-lateral blade of hyomandibular
LLB - lower left blade of the hyomandibular
LP2 - lower articulation in pharyngobranchial 2
L1 - laminae in first pterygiophore of first dorsal fin
MX - maxillary
MP - maxillary process
NS - neural spines
PR - parahypophysis
PA - parahypural
PC - postcleithrum
PH1-4 - pharyngobranchials 1 to 4
R - ribs
S - scapula
S1-4 - struts 1-4 of pharyngobranchial 3
UP - uncinate process of epibranchial 1
TLA - total length of opercular arm of hyomandibular
TLB - total length of the hyomandibular
URB - supero-posterior blade of the hyomandibular
UP2 - upper articulation in pharyngobranchial 2
X - X bone
Y - Y bone

pal caudal fin rays (PCR), lower procurrent caudal fin rays (LPCR), scales above lateral line (SALL), and scales below lateral line (SBLL). Lateral line scale counts were difficult to make and lateral body scale counts (LL) taken along the lateral midline, were preferentially recorded. Meristic characters were taken directly from the specimen, from dissected, cleared and stained specimens (Potthoff, 1984), or radiographs. Vertebral and caudal counts were not taken on specimens with regenerated caudal fins because only principal caudal rays are regenerated in morids. Osteological abbreviations used in the figures are presented in Table 1.

A cladistic approach to phylogenetic reconstruction, following Hennig (1966), was used. Polarity of character states was determined by out-groups (Watrous and Wheeler, 1981; Maddison et al., 1984). Essentially, characters with one or more states found in both outgroup and ingroup species were considered plesiomorphic (code 0). Code 9 was assigned to missing data. Ontogeny was used to help polarize pelvic fin ray counts following Nelson's (1978) logic: a character that changes from larvae to adults will have the larval state coded as plesiomorphic. This contrasts with the approach of Fahay and Markle (1984) and Markle (1989), who considered the ontogeny itself the character with states such as "ontogenetic increase in pelvic fin rays" or "ontogenetic decrease in pelvic fin rays". The absence of ontogenetic information for most species precludes the latter approach.

Phylogenetic data were analyzed with PAUP (Phylogenetic Analysis Using Parsimony) version 3.0 using both the Heuristic-search and Branch-and-Bound options (Swofford 1991), and MacClade version 3.0 (Maddison and Maddison 1992).

Results

Classification. —To facilitate presentation of results, the classification is presented first. Evidence for the arrangement is found in subsequent sections.

Laemonema Günther, 1862
- *Laemonema barbatulum* Goode and Bean, 1883 - p. 625
- *Laemonema goodebeanorum* new species - p. 639
- *Laemonema gracillipes* Garman, 1899 - p. 649
- *Laemonema macronema* new species - p. 638
- *Laemonema laureysi* Poll, 1953 - p. 643
- *Laemonema longipes* (Shmidt, 1938) - p. 645
- *Laemonema melanurum* Goode and Bean, 1896 - p. 631
- *Laemonema rhodochir* Gilbert, 1905 - p. 647
- *Laemonema robustum* Johnson, 1862 - p. 634
- *Laemonema verecundum* (Jordan and Cramer, in Gilbert, 1897) - p. 650
- *Laemonema yarrelli* (Lowe, 1838) - p. 636
- *Laemonema yuvto* Parin and Sazonov, 1990 - p. 650

Guttigadus Taki, 1953
- *Guttigadus globiceps* (Gilchrist, 1906) - p. 657
- *Guttigadus globosus* (Paulin, 1983) - p. 660
- *Guttigadus kongi* (Markle and Meléndez, 1988) - p. 652
- *Guttigadus latifrons* (Holt and Byrne, 1908a) - p. 656
- *Guttigadus nana* Taki, 1953 - p. 659
- *Guttigadus nudicephalum* (Trunov, 1990) - p. 662

incertae sedis (not treated in phylogenetic analysis)
- *Guttigadus nudirostre* (Trunov, 1990) - p. 663
- *Guttigadus squamirostre* (Trunov, 1990) - p. 664
- *Laemonemodes compressicauda* (Gilchrist, 1903) - p. 664

Phylogenetic analysis

Characters used in the cladistic analyses are numbered and summarized in Table 2. In the following text, the character number is placed in bold type in parentheses following initial mention. Values of morphometric and meristic characters used in the analysis (Table 3), the ranges of the meristic characters (Table 4), and the data matrix (Table 5) are summarized for reference.

Table 2. List of characters used for cladistic analysis.

1. Interorbital width.
2. Principal component analysis of D2, A, PCV and CV.
3. Number of pectoral fin rays.
4. Number of lower gill rakers.
5. Presence or absence of highly modified scales on lateral line.
6. Presence or absence of pharyngobranchial 1.
7. Presence or absence of pharyngobranchial 2.
8. Number of articulations on pharyngobranchial 2.
9. Presence/absence of uncinate process on epibranchial 1.
10. Presence/absence of interarcual cartilage.
11. Presence/absence of interarcual ligament.
12. Length of epibranchial 1 relative to epibranchial 2.
13. Presence/absence of groove between struts 3 and 4 on pharyngobranchial 3.
14. Shape of cartilage joining superior arms of pelvis.
15. Angle between superior and inferior arms of pelvis.
16. Presence/absence of pelvic foramen.
17. Number of visible pelvic fin rays.
18. Length of third pelvic ray relative to longest ray.
19. Total number of pelvic fin rays in adults.
20. Presence/absence of "neck" swim bladder.
21. Number of parapohyses associated with second chamber ofswimbladder.
22. Presence/absence of ligament between swim bladder and cranium.
23. Attachment of swim bladder cornua to skin.
24. Type of swim bladder cornua.
25. Presence/absence of a foramen on scapula-coracoid.
26. Length of coracoid arm.
27. Width of cartilagenous tip of coracoid arm.
28. Size of teeth in upper jaws.
29. Number of teeth in upper jaws.
30. Shape of maxillary process.
31. Presence/absence of posterior notch on maxillary.
32. Presence/absence of vomer.
33. Number of teeth on vomer.
34. Shape of vomer.
35. Ratio of hyomandibular length to length of its opercular arm.
36. Presence/absence of antero-lateral blade of hyomandibula.
37. Position of foramen in hyomandibula.
38. Length of supero-posterior blade of hyomandibula.
39. Length of antero-inferior blade of hyomandibula.
40. Number of upper procurrent caudal fin rays.
41. Number of lower procurrent caudal fin rays.
42. Number of preural vertebrae to base of first upperprocurrent caudal fin ray.
43. Number of preural vertebrae to base of first lowerprocurrent caudal fin ray.
44. Position of anus relative to origin of the anal fin.
45. Presence/absence of laminar bone on first pterygiophoreof first dorsal fin.
46. Number of the precaudal vertebrae opposite at the levelof the first anal fin ray.
47. Presence/absence of black stripe on dorsal fins.
48. Fleshiness of base of vertical fins.
49. Living depth.

Table 3. Average (X) and standard deviation (SD) for percentage of morphometric (in SL) and meristic character used in phylogenetic analysis (* = outgroups).

	Morphometric		Meristic character			
	INT		P1		LGR	
	X	SD	X	SD	X	SD
L. barbatulum	4.6	0.39	21.1	0.76	11.5	0.59
L. filodorsale	5.6	0.32	27.8	1.28	13.8	1.03
L. goodebeanorum	4.0	0.37	20.2	0.72	18.3	0.83
L. gracillipes	4.8	0.35	22.2	0.75	18.0	1.90
L. macronema	4.8	0.21	27.0	0.00	12.3	0.58
L. laureysi	3.8	0.33	20.8	0.85	18.5	0.96
L. longipes	6.5	0.35	16.9	0.79	19.8	0.96
L. melanurum	4.8	0.26	26.2	0.98	13.2	1.16
L. modestum	4.9	0.00	27.0	0.00	13.0	0.00
L. rhodochir	4.3	0.31	22.7	0.75	12.5	0.88
L. robustum	5.7	0.37	28.1	0.90	14.4	0.79
L. verecundum	4.2	0.46	18.7	0.47	13.0	0.82
L. yarrelli	4.3	0.43	22.9	1.14	16.2	0.84
L. yuvto	5.1	0.00	31.0	0.00	13.0	0.00
G. globiceps	9.3	0.92	19.1	2.53	25.8	2.56
G. globosus	14.0	0.85	24.5	0.70	19.0	1.00
G. kongi	9.6	1.47	24.1	1.23	16.4	1.95
G. latifrons	8.7	0.69	22.1	1.16	15.8	0.85
G. nana	6.1	0.51	23.2	0.60	4.7	0.65
G. nudicephalum	10.1	0.98	27.6	0.55	10.4	0.55
G. paulini	11.8	1.00	24.0	0.89	17.7	0.51
*A. marginatus**	4.4	0.00	22.0	0.00	18.0	0.00
*Le. eques**	5.8	0.00	22.0	0.00	14.0	0.00
*Lo. fernandeziana**	5.9	0.00	24.0	0.00	8.0	0.00
*P. fulvus**	6.6	0.00	24.0	0.00	8.0	0.00

MORPHOMETRIC AND MERISTIC CHARACTERS. —The interorbital width (**1**) of specimens greater than 50 mm was coded with two states, state 0 was narrow (3.0-7.0 % SL), the plesiomorphic state, and state 1 was wide (7.1-15.0 % SL) (Table 5). Two species, *L. melanurum* and *L. barbatulum*, represented by large sample sizes that included young "*Svetovidovia*" stages showed a decrease in relative interorbital width (from about 7-10% in *L. melanurum* smaller than 50 mm, to about 5% in larger specimens). *Guttigadus*, except *G. nana*, have a wide interorbital, the derived state, and all other taxa, including the outgroups, have a narrow interorbital (Fig. 1; Table 5). The regression relationship of interorbital width on standard length (50-250 mm) was: *Laemonema* (INT = 0.8+0.04SL, n = 260, $r^2 = 0.86$); *G. nana* (INT = 1.4+0.04SL, n = 9, $r^2 = 0.72$); and *Guttigadus* (INT = 2.6+0.12SL, n = 133, $r^2 = 0.73$). Although the sample size for *G. nana* was small, the identity of slopes for *Laemonema* spp. and *G. nana* suggests that the two have a similar ontogeny for this character.

Four meristic characters were found to be highly correlated: number of second dorsal fin rays, number of anal fin rays, number of precaudal vertebrae, and number of caudal vertebrae (**2**, Fig. 2), and were analyzed in a Principal Component Analysis (Fig. 3). Three groups were found; *Laemonema* and the outgroups fell together and were coded as state 0; most *Guttigadus* fell together and were coded state 1; and *G. nana* was separate, coded state 2. The character-state change from the *Laemonema* condition is a synapomorphy for all *Guttigadus*.

A low number of pectoral fin rays (**3**) (16-24), as found in all outgroups, was plesiomorphic, state 0, and a higher number (25-31) was derived, state 1 (Table 5). The derived state of a higher number of pectoral fin rays tended to be found in those *Laemonema* with a deep body, and the lower numbers in those with a narrow body. In *Guttigadus* this trend was not present.

A low number of gill rakers (4-8) on the lower limb of the first arch (**4**) was state 0, an intermediate number (9-21) was state 1, and a high number (more than 21) was state 2 (Tables 2,3). The outgroup analysis was equivocal (Table 5). This character does not vary much, only *G. globiceps* (22-30 LGR) and *G. nana* (4-6 LGR) were scored differently than other *Laemonema* and *Guttigadus*. The reduction in *G. nana* is similar to the reduction in serial meristic characters noted for **2** above.

OSTEOLOGICAL AND ANATOMICAL CHARACTERS (Table 2). —*Scales*. Two character states were identified for scale type on the lateral line (**5**), one type was little modified, state 0, and the other was highly modified, state 1. All outgroups had the plesiomorphic state (Table 5). The highly modified scales form a small tube surrounded by skin, with a wide opening anteriad, and a taper to small posteriad opening. Each scale supports a tapered, trumpet-shaped segment that is highly pigmented. The pigmentation makes the segments distinct in contrast to the paler body of preserved specimens. These scales seem restricted to *Guttigadus* (except *G. nana*) and *L. yuvto*. We include *L. yuvto* because Parin and Sazonov (1990) reported "... modified lateral line scales 29-30," and Sazonov (pers. comm., 1995) describes the scales as "tubular." A juvenile of *G. kongi* (NMNZ P 23396, 57 mm SL) has these modified scales formed, indicating that development began at least by the juvenile stage. The absence of modified scales in *G. nana*, which reaches a maximum of 73.1 mm SL, might be interpreted as the absence of a character that develops in late juvenile or early adult stages of ancestral *Guttigadus*.

Dorsal gill arches. The gill arch (Figs. 4-5) generally had four epibranchials and four pharyngobranchials. The first pharyngobranchial is variable in gadiforms (Markle 1989) (**6**), its presence scored as state 0 (Figs. 4, 5b) and its absence as state 1 (Figs. 5a, 5c). The outgroup analysis was equivocal because *Lepidion eques* lacked a first pharyngobranchial (Figs. 5d; Table 5). Both *G. nana* and *G. globiceps* also lacked a first pharyngobranchial (Figs. 5a and 5c).

The second pharyngobranchial has three states (**7**): well developed, state 0 (Figs.4a-c); small, state 1 (Fig. 4d); and absent, state 2 (Fig. 5a). The outgroup analysis for this character was equivocal (Figs. 5d-5e; Table 5). The only species without a second pharyngobranchial was *G. nana*. The presence of one upper articulation in pharyngobranchial two (**8**) (Figs. 4a, 4c-d, 5b-c) was considered as plesiomorphic, state 0, the presence of two upper articulations (Figs. 4b) was considered derived, state 1, and the absence of pharyngobranchial two in *G. nana* (Fig. 5a) was coded as state 2. All outgroups shared the plesiomorphic condition (Figs. 5d-e; Table 5).

Table 4. Summary of meristic ranges for *Laemonema*, *Guttigadus* and outgroups.

Species	Meristic ranges			
	DI	D2	A	P1
L. barbatulum	6 - 7	57 - 63	54 - 63	19 - 23
L. goodebeanorum	6	66 - 73	65 - 71	19 - 22
L. gracillipes	6	56 - 63	55 - 61	21 - 23
L. macronema	6	57 - 58	54 - 55	27
L. laureysi	5 - 7	63 - 72	60 - 69	19 - 23
L. longipes	6	49 - 53	48 - 52	16 - 18
L. melanurum	7	53 - 61	52 - 59	25 - 27
L. rhodochir	6	61 - 66	58 - 63	22 - 24
L. robustum	6	50 - 57	48 - 54	26 - 30
L. verecundum	8 - 9	40 - 42	41 - 42	18 - 19
L. yarrelli	6	58 - 62	57 - 62	21 - 25
L. yuvto	6	62	53	31
G. globiceps	4 - 7	65 - 77	60 - 74	18 - 21
G. globosus	4 - 6	70 - 86	73 - 84	23 - 29
G. kongi	4 - 7	62 - 78	61 - 75	22 - 27
G. latifrons	5 - 6	64 - 76	61 - 76	21 - 26
G. nana	4 - 6	45 - 54	46 - 53	22 - 24
G. nudicephalum	4 - 5	59 - 62	56 - 60	27 - 28
	PCV	CV	TV	UGR
L. barbatulum	13 - 15	37 - 42	50 - 56	3 - 6
L. goodebeanorum	15 - 17	39 - 43	56 - 59	7 - 9
L. gracillipes	15 - 16	37 - 38	52 - 54	6 - 8
L. macronema	14	35 - 37	49 - 51	4 - 5
L. laureysi	14 - 17	38 - 43	53 - 58	5 - 8
L. longipes	14 - 16	34 - 37	49 - 52	7 - 8
L. melanurum	15 - 16	38 - 42	53 - 57	4 - 6
L. rhodochir	15	36 - 39	51 - 54	4 - 6
L. robustum	13 - 15	34 - 38	47 - 52	4 - 7
L. verecundum	12 - 13	29 - 31	42 - 43	5 - 6
L. yarrelli	15 - 17	36 - 39	52 - 56	6 - 8
L. yuvto	15	36	51	5
G. globiceps	11 - 13	44 - 50	55 - 62	10 - 13
G. globosus	12 - 14	42 - 47	56 - 59	6 - 8
G. kongi	10 - 13	37 - 44	49 - 56	6 - 10
G. latifrons	10 - 13	41 - 49	54 - 61	7 - 8
G. nana	10 - 12	27 - 30	39 - 41	1 - 2
G. nudicephalum	12 - 13	36 - 38	48 - 51	3 - 5

There are four epibranchials in all species studied. The first epibranchial may have an uncinate process (**9**), state 0 (Figs. 4a-c, 5b), or not have an uncinate process, state 1 (Figs. 4b, 5a, 5c). The outgroup analysis was equivocal (Figs. 5d-e; Table 5). Markle (1989) indicated that the presence of an uncinate process is a primitive condition for batrachoidiforms fishes which are the out-group of gadiform fishes within paracanthopterygians.

Table 4. Continued.

Species	Meristic ranges			
	LGR	UPPCR	LPCR	LL
L. barbatulum	10 - 13	7 - 9	14 - 20	128 - 140
L. goodebeanorum	17 - 20	8 - 11	12 - 16	125 - 143
L. gracillipes	16 - 21	8 - 9	12 - 14	155 - 172
L. macronema	12 - 13	8	11 - 13	125 - 126
L. laureysi	16 - 21	7 - 10	10 - 15	120 - 140
L. longipes	18 - 20	7 - 8	9 - 11	110 - 144
L. melanurum	12 - 15	7 - 10	11 - 15	145 - 166
L. rhodochir	11 - 14	7 - 10	11 - 13	105 - 130
L. robustum	13 - 16	10 - 12	12 - 17	120 - 150
L. verecundum	11 - 14	10 - 11	13	no data
L. yarrelli	14 - 18	6 - 7	10 - 12	100 - 111
L. yuvto	13	no data	no data	35
G. globiceps	22 - 30	7 - 9	9 - 12	85 - 105
G. globosus	17 - 20	10 - 12	13 - 15	111 - 137
G. kongi	13 - 21	8 - 12	10 - 14	170
G. latifrons	14 - 17	10 - 12	12 - 14	145 - 150
G. nana	4 - 6	7 - 8	9 - 10	60 - 75
G. nudicephalum	10 - 11	11 - 12	12 - 14	114 - 135
	SALL	SBLL		
L. barbatulum	12 - 15	21 - 30		
L. goodebeanorum	10 - 13	no data		
L. gracillipes	14 - 15	30 - 35		
L. macronema	10 - 11	23 - 24		
L. laureysi	10 - 13	22		
L. longipes	10 - 11	20 - 25		
L. melanurum	18	35 - 36		
L. rhodochir	9 - 15	21		
L. robustum	14 - 19	39 - 47		
L. verecundum	no data	no data		
L. yarrelli	8 - 9	18 - 23		
L. yuvto	13	no data		
G. globiceps	7 - 8	15 - 25		
G. globosus	12	7		
G. kongi	12	35		
G. latifrons	14	38		
G. nana	8	no data		
G. nudicephalum	18 - 20	40 - 55		

The presence of an interarcual cartilage (**10**), considered a derived state for gadiform fishes (Markle 1989), was absent in some species, state 0 (Figs. 5a-c) and present in others, state 1 (Figs. 4a-d). The outgroup analysis was equivocal (Figs. 5d-e; Table 5). The interarcual cartilage is sustained generally by an interarcual ligament, which is connected with the uncinate process and the non-ossified area of the first epibranchial. The interarcual ligament (**11**) was present, state 1 (Figs. 4a, 4d) or absent, state 0 (Figs. 4b-c, 5a-c). The outgroup analysis was equivocal (Figs. 5d-e and Table 5).

Table 5. Data matrix for cladistic analysis (* = outgroups)

Taxa	Characters				
	1	1111111112	2222222223	3333333334	444444444
	1234567890	1234567890	1234567890	1234567890	123456789
L. barbatulum	0001000001	1100002200	0100001101	0100101111	010011010
L. goodebeanorum	0001000001	0100002200	0100000001	1100001111	110010000
L. gracillipes	0001000101	1100002200	2100000001	0110001011	100090000
L. macronema	0011000001	0110012201	0101001011	0100001111	110001000
L. laureysi	0001000001	0100002200	0100000001	1100001010	100010000
L. longipes	0001001011	1100102212	2111100010	2101111011	101011000
L. melanurum	0011000001	1100002200	0100101001	0100001011	100010000
L. rhodochir	0001000101	0100002200	0100001011	0100001011	111010000
L. robustum	0011000101	1010012201	0101001011	0110101010	100010000
L. verecundum	0001000001	1100002212	2110001010	2101001000	199091000
L. yarrelli	0001000001	1100002200	0100000001	0100101011	110010010
L. yuvto	0011199999	9999992299	9999999099	9190999999	999199000
G. globiceps	1102110010	0101001210	1000011000	1100111111	111101100
G. globosus	1101100011	1001101110	1000011000	1100111010	100111100
G. kongi	1101100010	1101101110	1000011100	1100111010	100111100
G. latifrons	1101100000	0001001110	1000111000	1100111110	100101100
G. nana	0200012210	0000101212	2001110000	0022100111	111001001
G. nudicephalum	1111100010	0001101110	1100011200	1111111110	100111100
*Lo. fernandeziana**	0000000010	0100000000	0001001201	0022100000	000010001
*A. marginatus**	0001001010	0000001110	0000010000	0022000000	000010000
*Le. eques**	0001010001	1100000000	0100111001	0110111100	000020000
*P. fulvus**	0000000000	1001000000	0000000010	1022000111	111011000

Two character states were found for the maximum length of the first epibranchial (**12**), expressed as percentage of the second epibranchial, 90-120% was state 1 (Figs. 4a-d, 5b) and less than 90% was state 0 (Figs. 5a, 5c). The outgroup analysis was equivocal (Figs. 5d-e; Table 5).

The presence of a groove on strut 3 and 4 (**13**) was a derived state, state 1 (Figs. 5c), found only in *L. macronema* and *L. robustum*; the absence was plesiomorphic, state 0 (Figs. 4a-b, 4d, 5a-c). The outgroup analysis was decisive because all outgroups share the plesiomorphic state (Figs. 5d-e; Table 5).

In the five epibranchial/interarcual characters *Laemonema* tend to be more conservative and *Guttigadus* more variable, mainly in reductions or losses of the uncinate process, interarcual cartilage or interarcual ligament. *Guttigadus nana* again showed the most reductions and losses, possibly indicating neotenic or paedomorphic ancestry.

Pelvic girdle. The pelvic girdle (Figs. 6a-g) is formed by the basipterygia and has two pairs of arms, the superior arm of which is united to its opposite member by a cartilaginous joint, and a free inferior arm. The cartilaginous joint (**14**) had two states with an anteriorly directed projection, state 0 (Figs. 6a-c, 6e), and without, state 1 (Figs. 6d, 6f). The outgroup analysis was equivocal (Figs. 6g; Table 5). The angle between the two arms (**15**), could be categorized as less than 90° (Figs. 6a-c, 6f), the plesiomorphic condition, state 0, or equal or greater than 90° (Figs. 6d-e), the derived state, state 1. All the outgroups share an angle of less than 90° (Figs. 6g; Table 5).

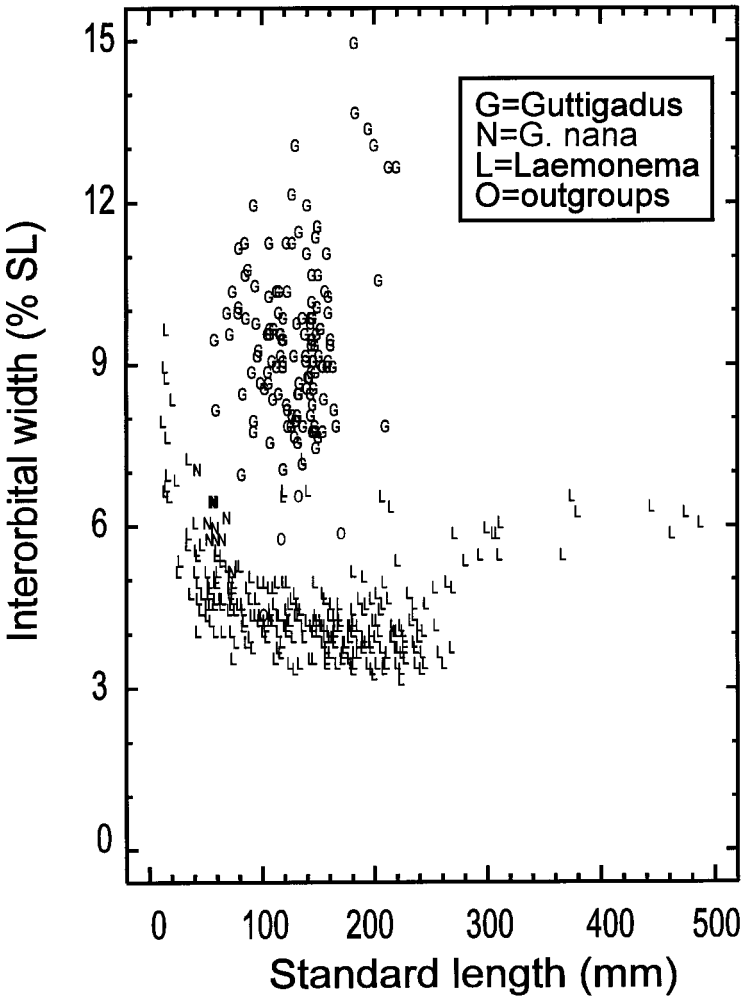

Figure 1. Interorbital width as percent SL vs SL (mm) for *Laemonema* (L), *Guttigadus* (G), *Guttigadus nana* (N), and outgroups (O).

The blade of the inferior arm (**16**) normally lacks a foramen and is considered the plesiomorphic condition because of its absence in outgroups (Fig. 6g; Table 5), state 0 (Fig. 6b, 6c-f), whereas the presence of a foramen on the blade was considered derived (Fig. 6a) state 1 and is present only in *L. macronema* and *L. robustum.*

Markle (1989) indicated that gadiform fishes have three pelvic fin-ray ontogenies, one occurs in some morids which have the following ontogeny N ≥ N+n1 ≥ N+n1-n2, where N is the primordial number of rays first countable, and the n's are subsequent additions or deletions. Adults of *Laemonema* have only two visible large pelvic fin rays (**17**) (Fig. 6a-b) and adults of most *Guttigadus* have three to five visible large pelvic fin rays (Figs. 6d-f). However, cleared and stained adult *Laemonema* may have one to nine small, inner pelvic rays (Fig. 6c). This evidence, plus the juvenile stage of *L. barbatulum* discussed below, indicated that there is a reduction in pelvic fin ray size during ontogeny from

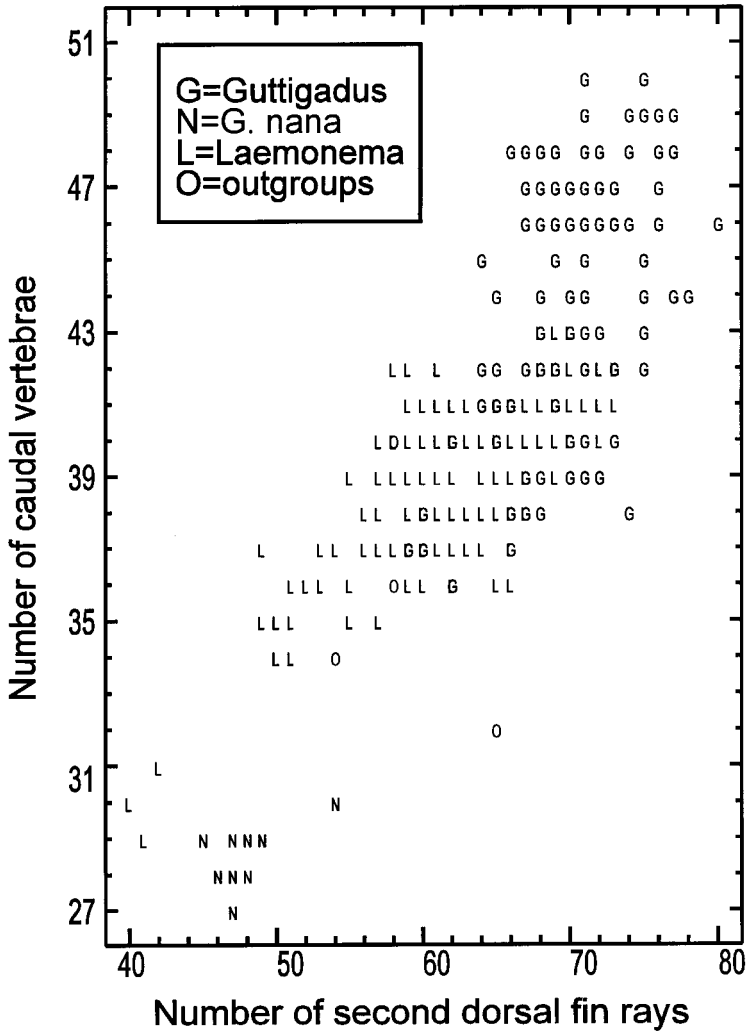

Figure 2. Relationship between number of caudal vertebrae and number of second dorsal fin rays for *Laemonema* (L), *Guttigadus* (G), *Guttigadus nana* (N), and outgroups (O).

juvenile to adult. The outgroups had five or more large visible pelvic fin rays, and the outgroup analysis was equivocal (Figs 6g; Table 5). Because outgroups and early ontogenetic stages of the ingroup usually have five or more large visible pelvic fin rays, we polarized the character. A number greater than five was considered plesiomorphic (state 0), and there were two unordered derived states: five to three (state 1), and fewer than three (state 2).

The ratio of the length of the third to the length of the largest pelvic fin ray (**18**) showed three states: more than 40%, state 0; 15-40%, state 1 (Figs. 6d); and less than 15%, state 2 (Figs. 6a-b, 6e-f). The outgroup analysis was equivocal (Figs 6g; Table 5).

The total number of all adult pelvic fin rays, including those only seen in cleared and stained specimens (**19**), showed two character states, five or less was state 1 (Figs. 6d-f), and seven or more was state 0 (Figs. 6a-c). The outgroup analysis was equivocal (Figs.

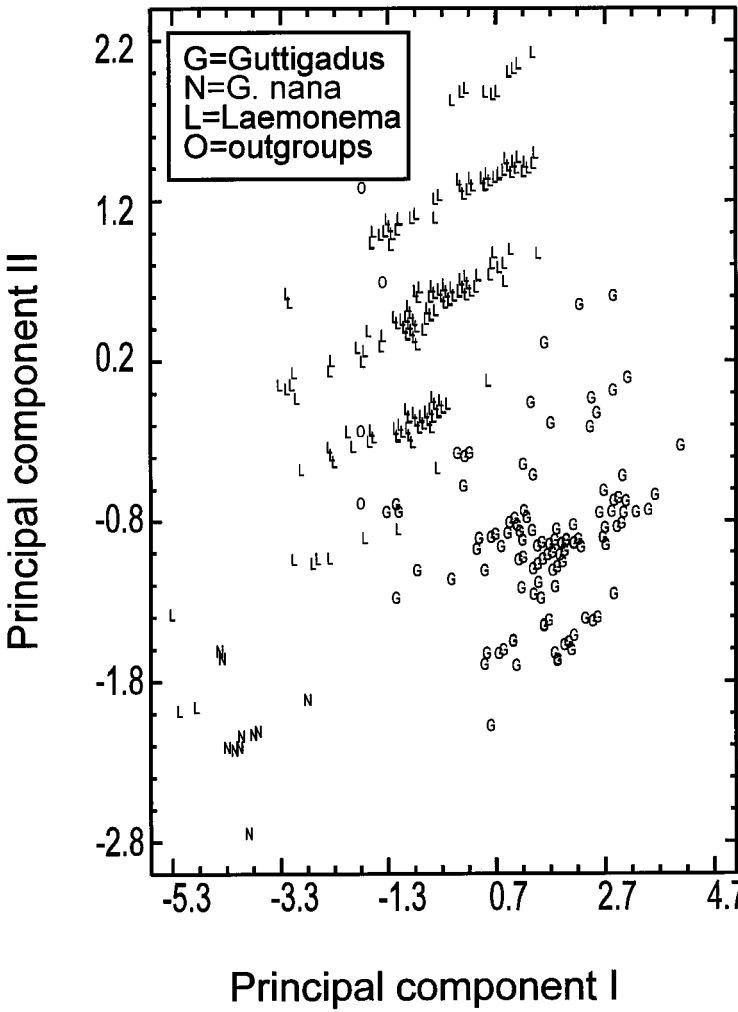

Figure 3. Principal component analysis using PCV, CV, D2 and A for *Laemonema* (L), *Guttigadus* (G), *Guttigadus nana* (N), and outgroups (O).

6g; Table 5). The total number of pelvic fin rays ranges from 4-12 in *Laemonema*, and 3-5 in *Guttigadus*.

Swimbladder. The swimbladder of all morids has direct contact with the otic area of the cranium (Figs. 7-8). This characteristic appears to have evolved in many groups of fishes, but in Gadiformes is restricted to morids (Paulin, 1988). Paulin (1988) indicated that morids have an anterior and a posterior chamber separated by a constriction (neck) at the level of the parapophyses of the fourth vertebra.

We found variability in constriction presence and length, involving the fourth to the seventh parapophyses. When absent, we can not distinguish whether these species have lost the neck or lost the second chamber and expanded the neck. In spite of this uncertainty regarding homology, we will interpret the structure as loss of the neck. An elongate neck on the swimbladder (**20**) was considered plesiomorphic (state 0, Figs. 7a, 8a-b), because all outgroups had an elongate neck (Figs. 8c-d; Table 5); a small neck was state 1

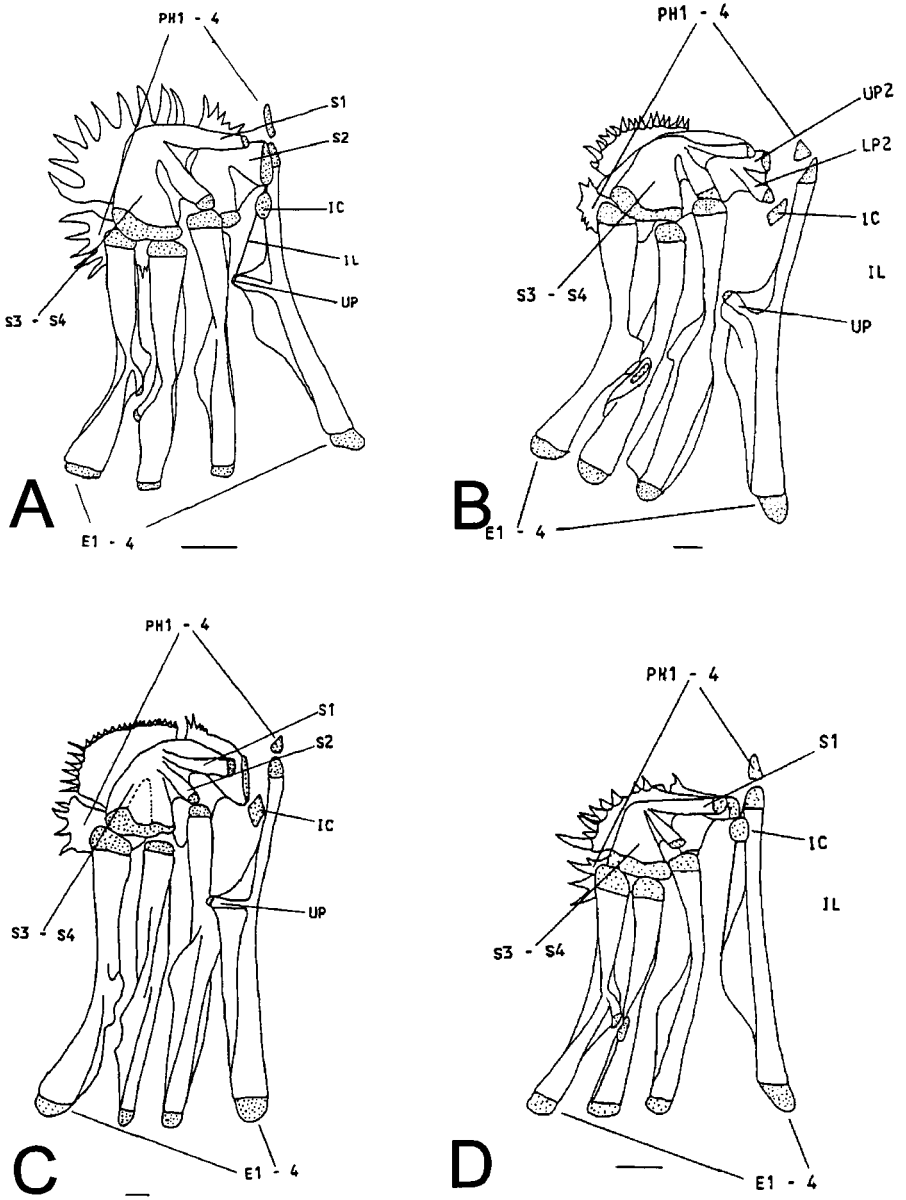

Figure 4. Dorsal view of right gill arches, anterior to right, scale = 1 mm. A. *Laemonema barbatulum* (UF 13120), B. *Laemonema gracillipes* (USNM 135362), C. *Laemonema macronema* (RUSI 1423), D. *Laemonema longipes* (CAS 47657).

(Fig 7b), and absence of the neck in *L. longipes, L. verecundum* and *G. nana* was state 2 (Figs. 7d-e).

The number of parapophyses (**21**) associated with the posterior chamber was divided into three states. All outgroups had seven or more parapophyses (Figs. 8c-d; Table 5). Thus, we coded seven or more parapophyses as plesiomorphic (state 0, Figs. 7a-b), fewer

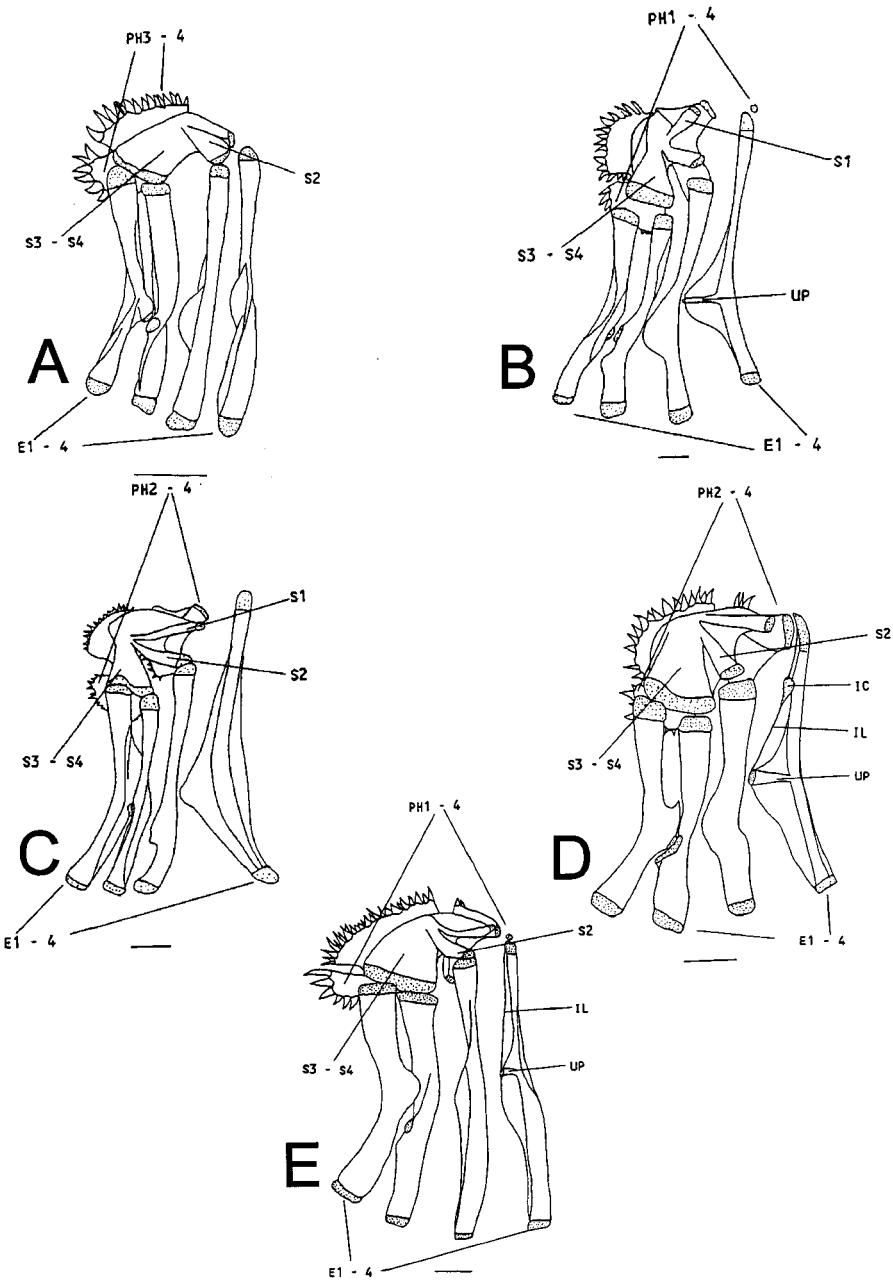

Figure 5. Dorsal view of right gill arches, anterior to right, scale = 1 mm. A. *Guttigadus nana* (UMMZ 214588), B. *Guttigadus latifrons* (MSU. uncat.), C. *Guttigadus globiceps* (MSU uncat.), D. *Lepidion eques* (USNM 211787), E. *Physiculus fulvus* (USNM 232481).

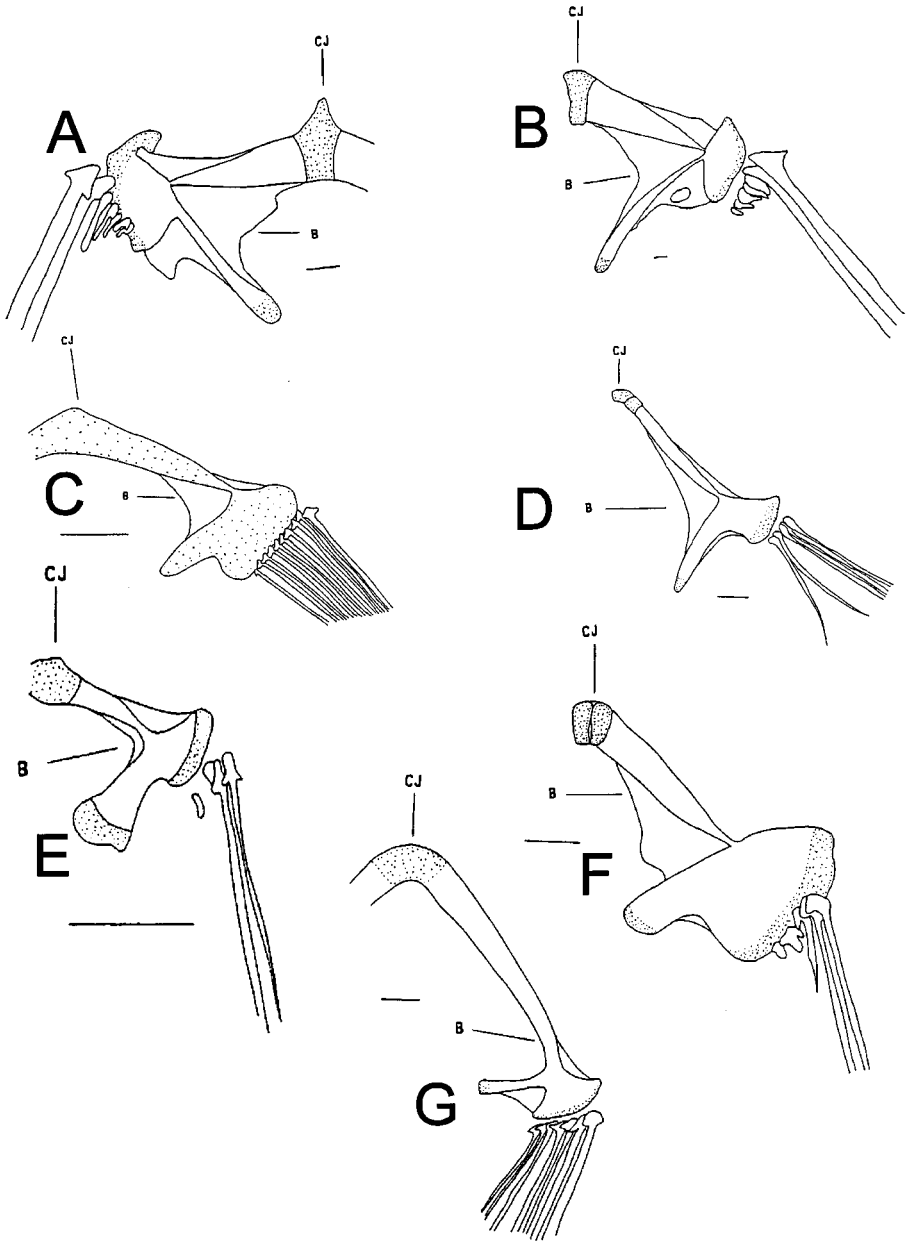

Figure 6. Dorsal view of pelvic girdle, scale = 1 mm. A. *Laemonema laureysi* (IRSB 175), B. *Laemonema macronema* (RUSI 1423), C. *Laemonema barbatulum* juvenile (ARC uncat.), D. *Guttigadus kongi* (MNHNC P. 6589), E. *Guttigadus nana* (UMMZ 214588), F. *Guttigadus globiceps* (MSU uncat.), G. P*hysiculus fulvus* (USNM 232481).

than seven derived (state 1, Figs. 8a-b), and for those with no posterior chamber (state 2, Fig. 7c-e). The derived state 1 is a synapomorphy for all *Guttigadus*, except *G. nana*.

A small patch of ligament on each cornua of the swimbladder and the posterior edges of the cranium (**22**) was either present (state 0, Figs. 7e, 8b) or absent (state 1, Figs. 7a-d,

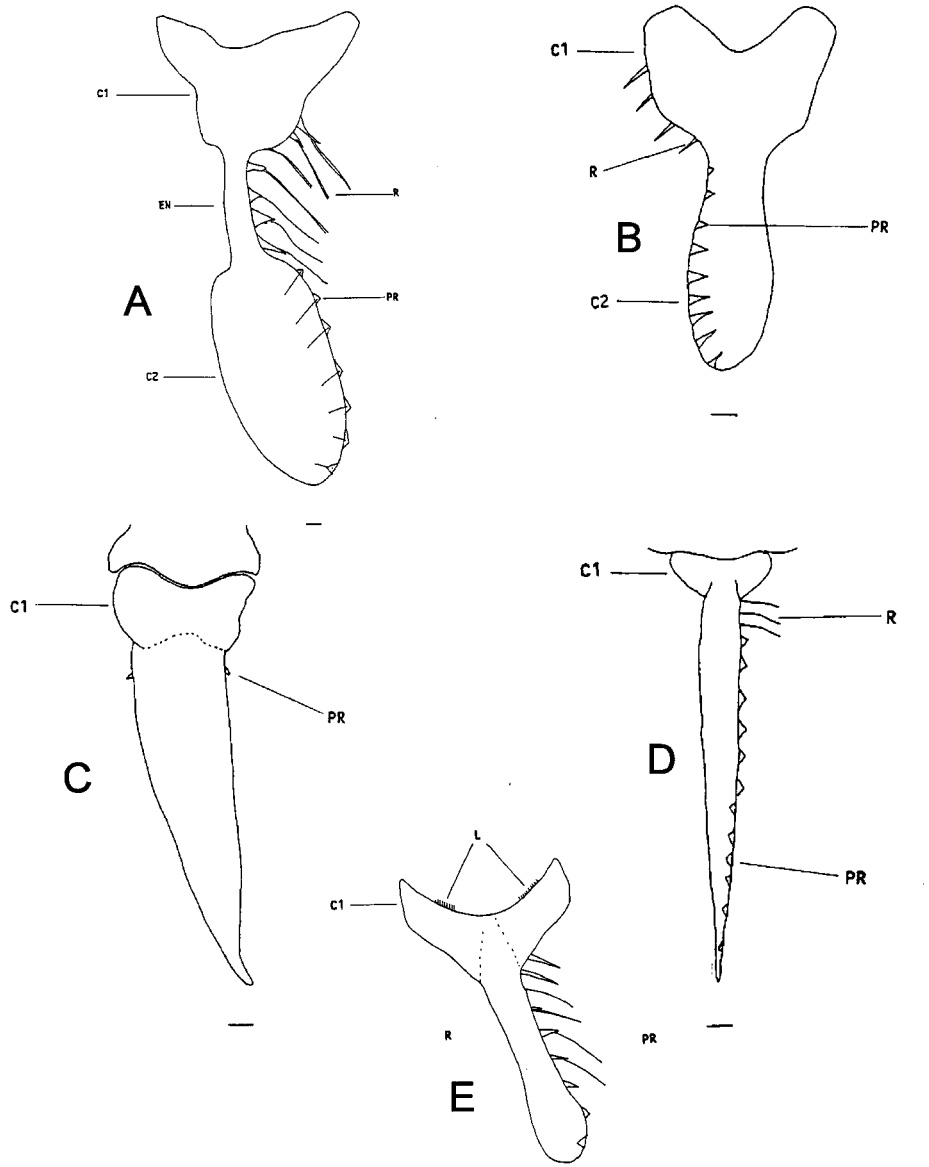

Figure 7. Ventral view of swimbladder, anterior to top. A. *Laemonema barbatulum* (UF 13120), scale = 1 mm, B. *Laemonema robustum* (MMF 3128), scale = 1 cm, C. *Laemonema verecundum* (LACM 31118-2), scale = 1 mm, D. *Laemonema longipes* (HUMZ 81033), scale = 1 cm, E. *Guttigadus nana* (UMMZ 214588), scale = 1 mm.

8a). The outgroup analysis was equivocal (Figs. 8c-d; Table 5). The cornua may be in contact with the skin at each side of the head (**23)** (state 0, Figs. 7a-b, 7e, 8a-b) or not in contact, the derived state 1 (Figs. 7c-d). All outgroups shared the plesiomorphic condition (Figs. 8c-d; Table 5). Two shapes of the cornua (**24**) were found; the cylindrical shape was state 1 (Figs. 7b, 7d-e), and the triangular shape was state 0 (Figs. 7a, 7c, 8a-b). The outgroup analysis was equivocal (Figs. 8c-d; Table 5).

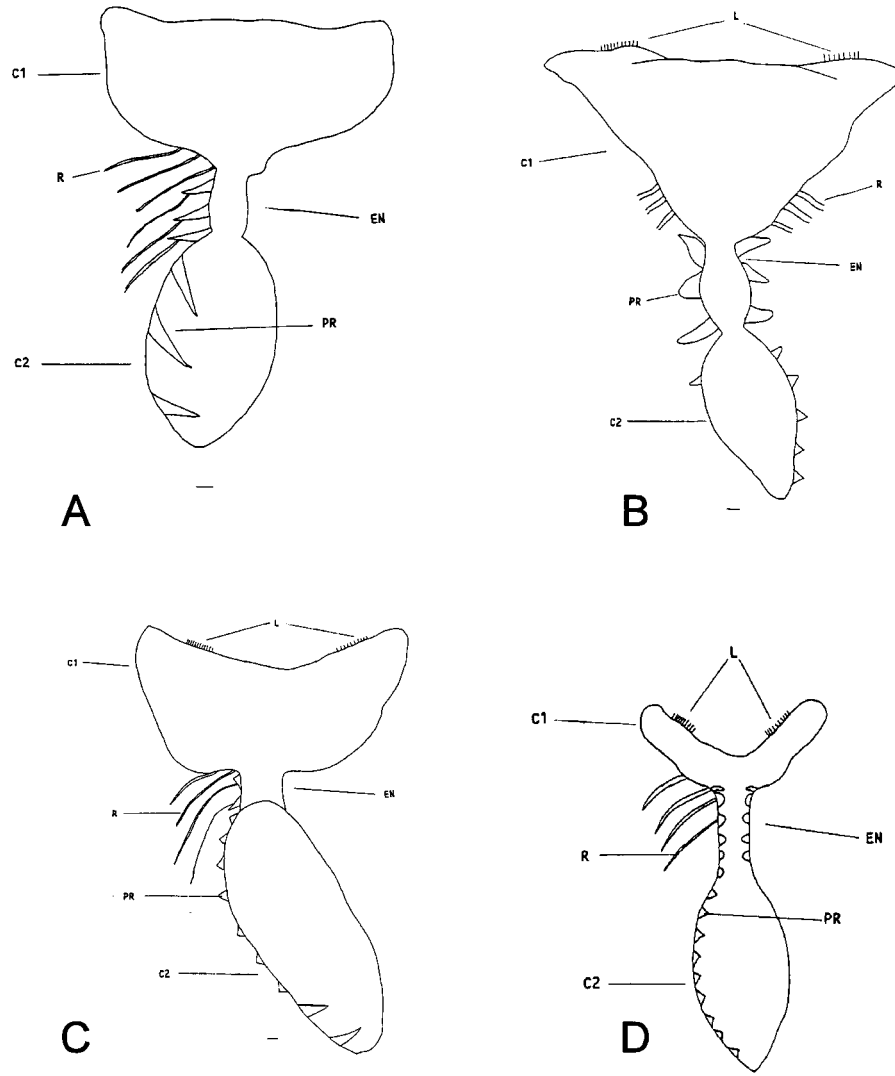

Figure 8. Ventral view of swimbladder, anterior to top, scale = 1 mm. A. *Guttigadus nudicephalum* (MSU uncat.), B. *Guttigadus latifrons* (MSU uncat.), C. *Physiculus fulvus* (USNM 232481), D. *Lotella fernandeziana* (CAS 24144).

Pectoral girdle. According to Markle (1989) the presence of a foramen located between the scapula and coracoid (Figs. 9a-f), is a derived character in gadiforms. This character can be referred to as either a foramen in both bones (**25**), state 0 (Figs. 9a-b, 9d), or a foramen in the scapula bone, state 1 (Figs. 9c, 9e). The outgroup analysis was equivocal (Fig. 9f; Table 5).

The lower arm of the coracoid (**26**) had two states, long relative to the cleithrum length (state 0, Figs. 9a-c), and short (state 1, Figs. 9d-e). The outgroup analysis was equivocal (Figs. 9f; Table 5). The width of shaft of the lower arm of the coracoid (**27**) either was uniform along its length, state 0 (Figs. 9b-c, 9e), or was wider at its cartilaginous distal tip

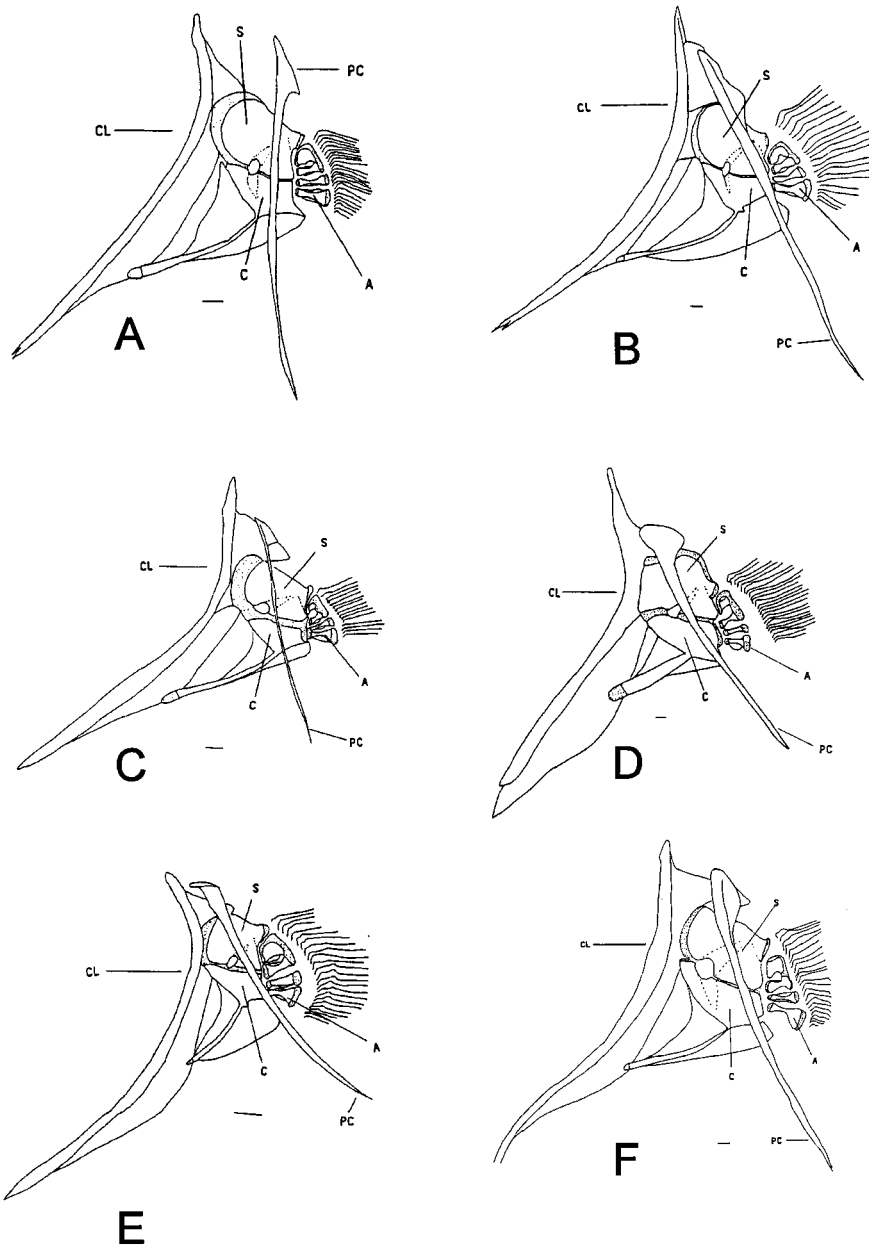

Figure 9. Medial view of right pectoral girdle, anterior to left, scale = 1 mm. A. *Laemonema barbatulum* (UF 13120), B. *Laemonema laureysi* (IRSB 175), C. *Laemonema longipes* (CAS 47657), D. *Guttigadus globosus* (NMNZ 25203), E. *Guttigadus nana* (UMMZ 214588), F. *Lotella fernandeziana* (CAS 24144).

than near the base of the coracoid plate, state 1 (Figs. 9a, 9d). The outgroup analysis was equivocal (Figs. 9f; Table 5).

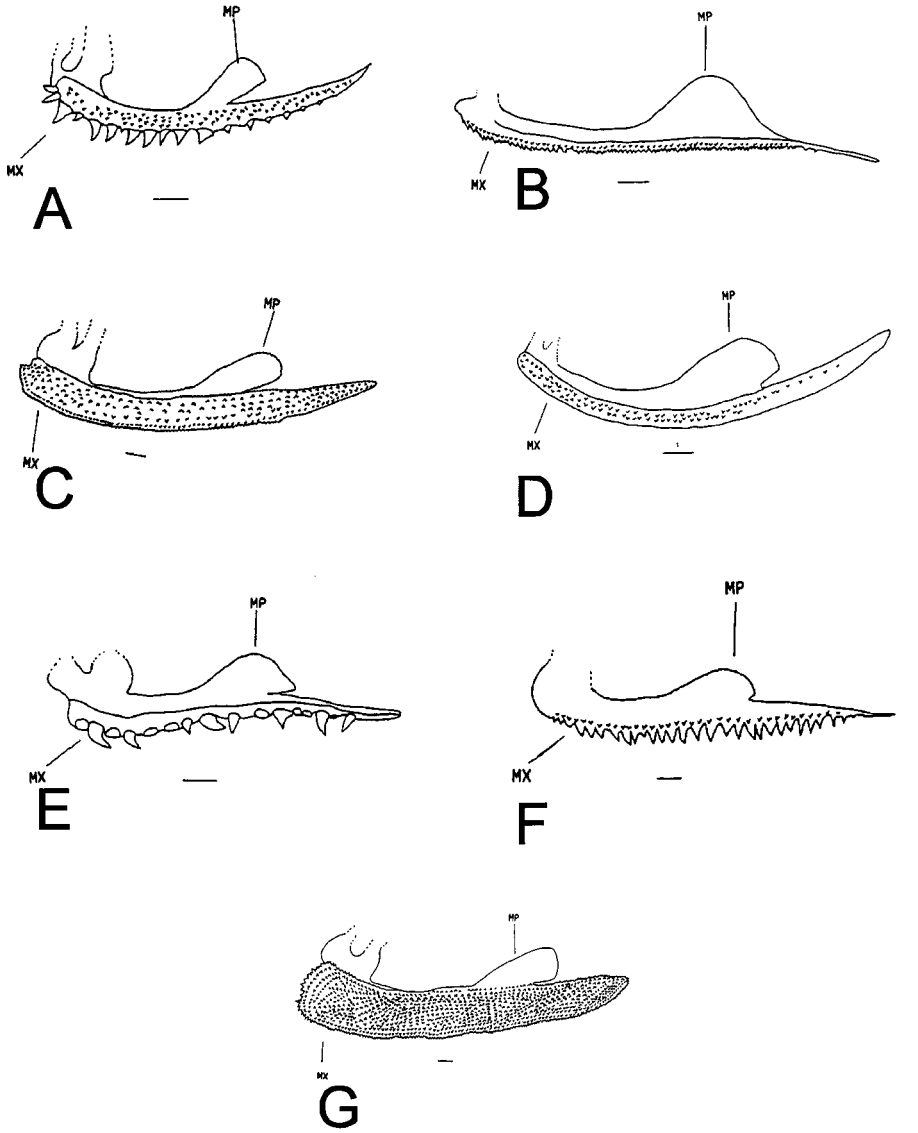

Figure 10. Medial view of right maxillary, scale = 1 mm. A. *Laemonema barbatulum* (UF 13120), B. *Laemonema longipes* (CAS 47657), C. *Laemonema rhodochir* (PPSIO uncat.), D. *Guttigadus globosus* (NMNZ 25203), E. *Guttigadus nudicephalum* (MSU uncat.), F. *Guttigadus kongi* (MNHNC P 6589), G. *Laemonema macronema* (RUSI 1423).

Upper jaws and vomer. In the upper jaw there are multiple rows of teeth (**28**) which may be uniform, minute and caniniform (Figs. 10b-d, 10g), state 0; have an external row of caniniform teeth at least three times the size of inner, minute teeth (Figs. 10a, 10f), state 1; or have an external row of strong caniniform teeth at least five times the size of inner, minute teeth (Fig. 10e), state 2. Outgroup analysis was equivocal (Table 5). The number of teeth on the external row of one side of the upper jaw (**29**) was more than 50, state 1, or less than 50, state 0. Outgroup analysis was equivocal (Table 5).

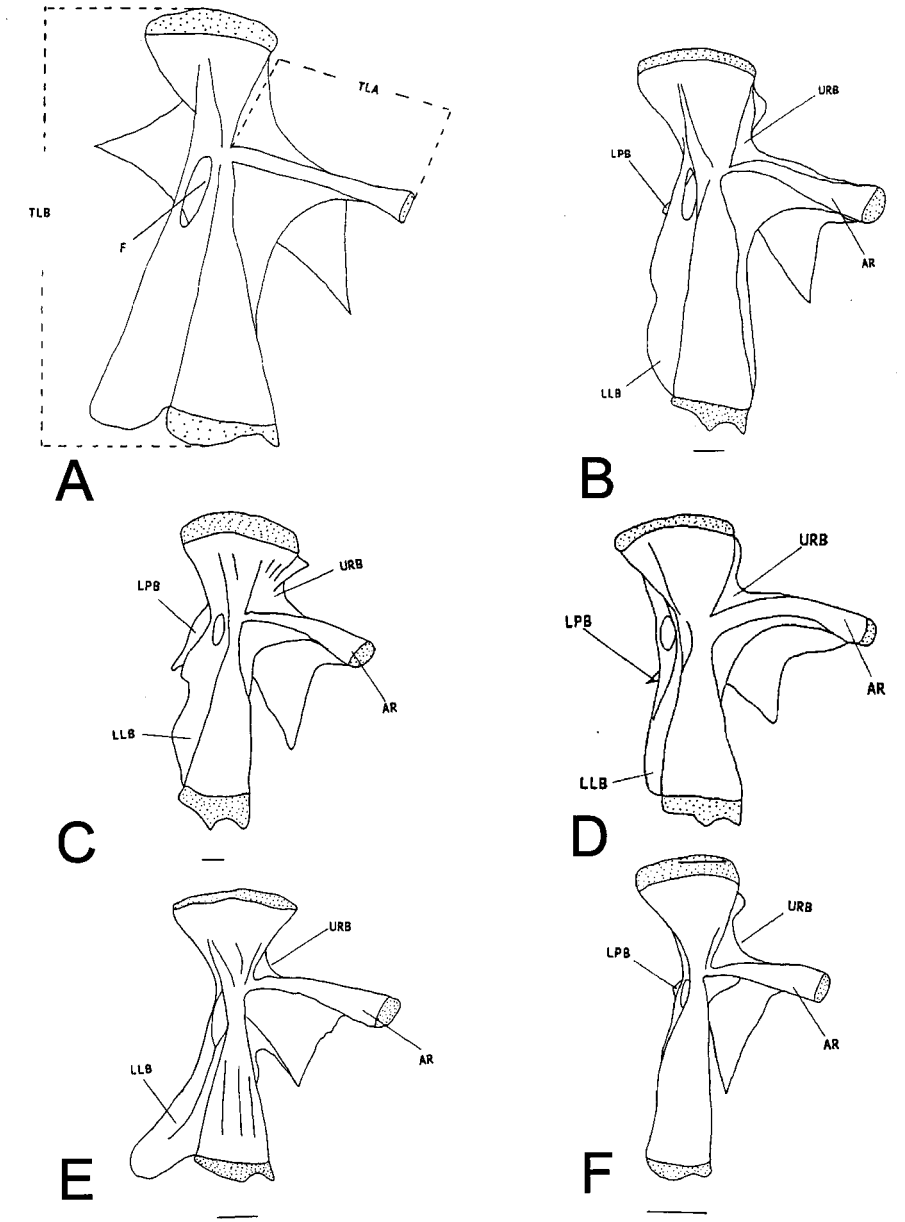

Figure 11. Medial view of right hyomandibula, anterior to left, scale = 1 mm. A. Schematic showing measurements, B. *Laemonema goodebeanorum* (UF 44476), C. *Laemonema gracillipes* (USNM 135362), D. *Laemonema melanurum* (USNM 30441), E. *Laemonema longipes* (CAS 47657), F. *Laemonema verecundum* (LACM 31118-2).

The shape of the maxillary process (**30**) was rounded, state 0 (Fig. 10b, 10d-f), or rectangular, state 1 (Fig. 10a, 10c, 10g). The outgroup analysis was equivocal (Table 5). A posterior notch in the maxillary process (**31**) was scored as deep, state 0 (Fig. 10a, 10c,

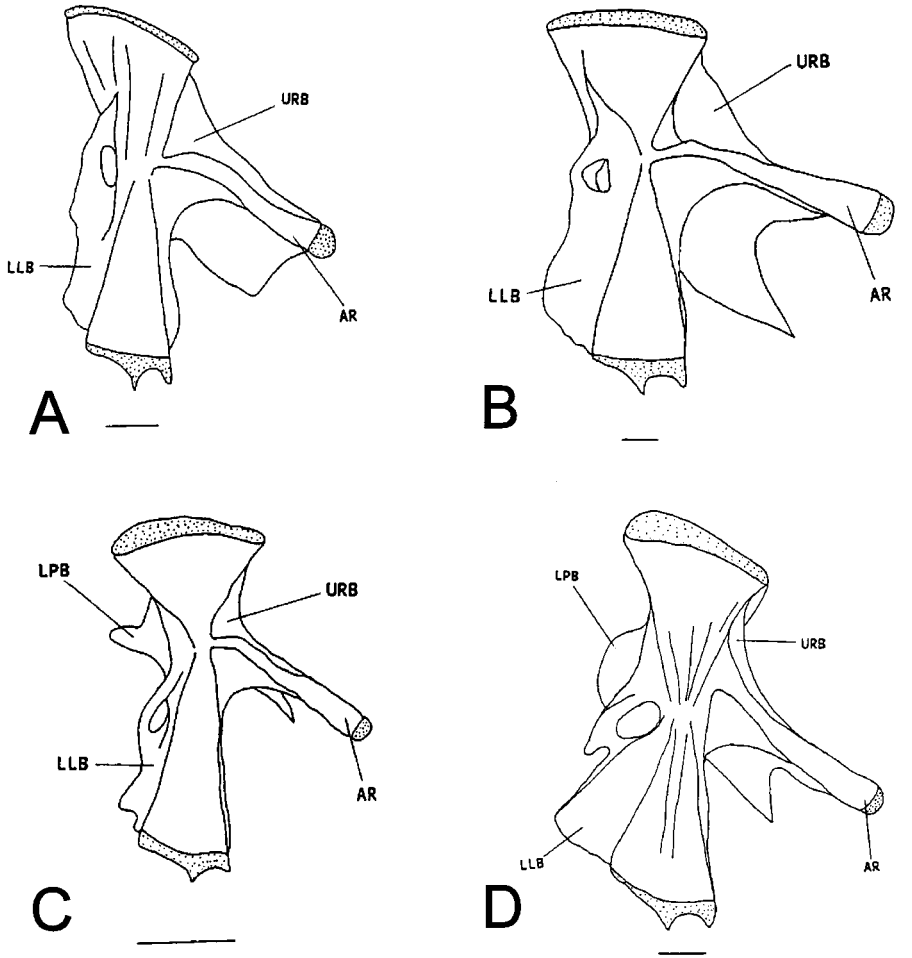

Figure 12. Medial view of right hyomandibula, anterior to left, scale = 1 mm. A. *Guttigadus globiceps* (MSU uncat.), B. *Guttigadus kongi* (MNHNC P6589), C. *Guttigadus nana* (UMMZ 214588), D. *Physiculus fulvus* (USNM 232481).

10g), shallow, state 1 (Fig. 10d-f), or absent, state 2 (Fig. 10b). The outgroup analysis was equivocal (Table 5).

The vomer (**32**) was either absent as in *G. nana*, state 0, or present, state 1. The outgroup analysis was equivocal (Table 5). When present, the shape of the vomer (**34**) was either rounded (most species), state 0, or v-shaped as in *L. longipes*, *L. verecundum* and *G. nudicephalum*, state 1. Those species with no vomer were coded as state 2. The outgroup analysis was equivocal (Table 5). The number of teeth on the vomer (**33**) was coded as 0 when there were 10 or fewer, and state 1 when there 11 or more. Again, those species with no vomer were coded as state 2. The outgroup analysis was equivocal (Table 5).

Hyomandibular bone. A hypothetical hyomandibular bone is showed in Figure 11a to facilitate the understanding of the following characters related to this bone (Figs. 11-12). A ratio between the total length of the body of the hyomandibular bone and the total

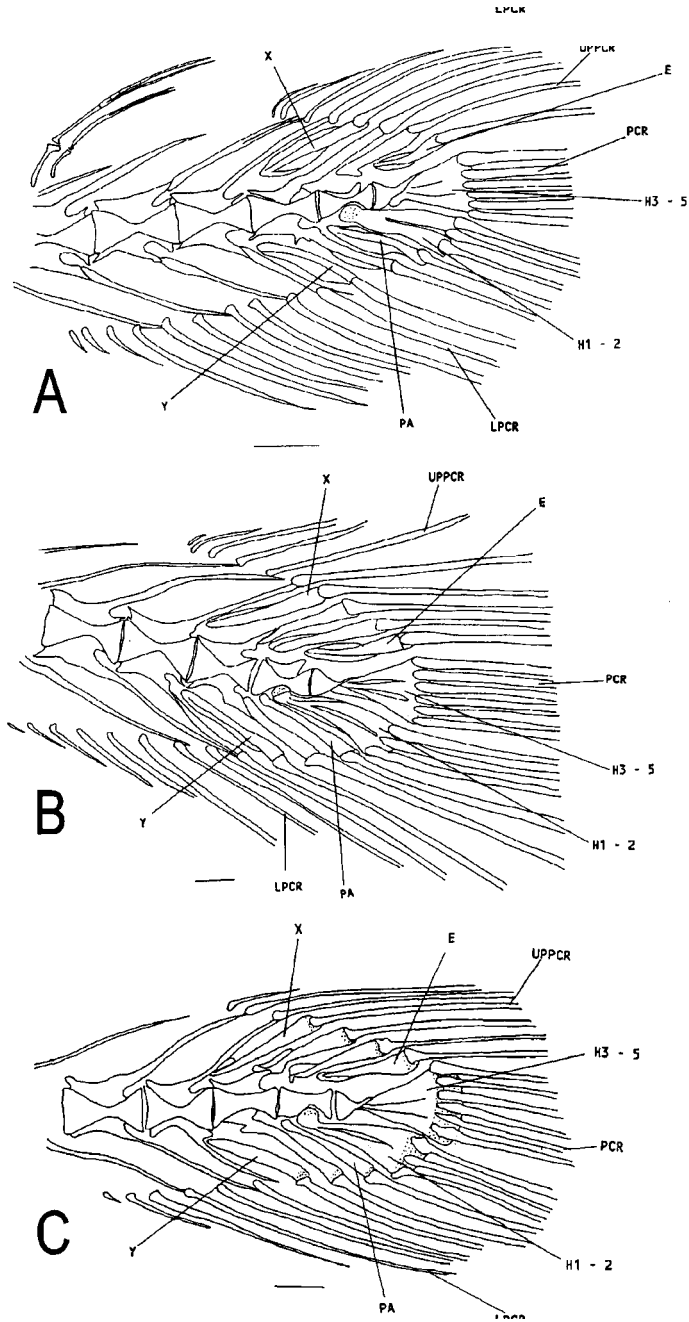

Figure 13. Left lateral view of caudal skeleton, scale = 1 mm. A. *Laemonema barbatulum* (UF 13120), B. *Laemonema laureysi* (IRSB 175), C. *Laemonema gracillipes* (USNM 135362).

length of the opercular arm (**35**) greater than 50.0% was state 1 (Figs. 11e, 12a-c), and less than 50.0% was state 0 (Figs. 11b-d, 11f). The outgroup analysis was equivocal (Fig. 12d; Table 5). The presence of an antero-lateral blade behind the body of the hyomandibular

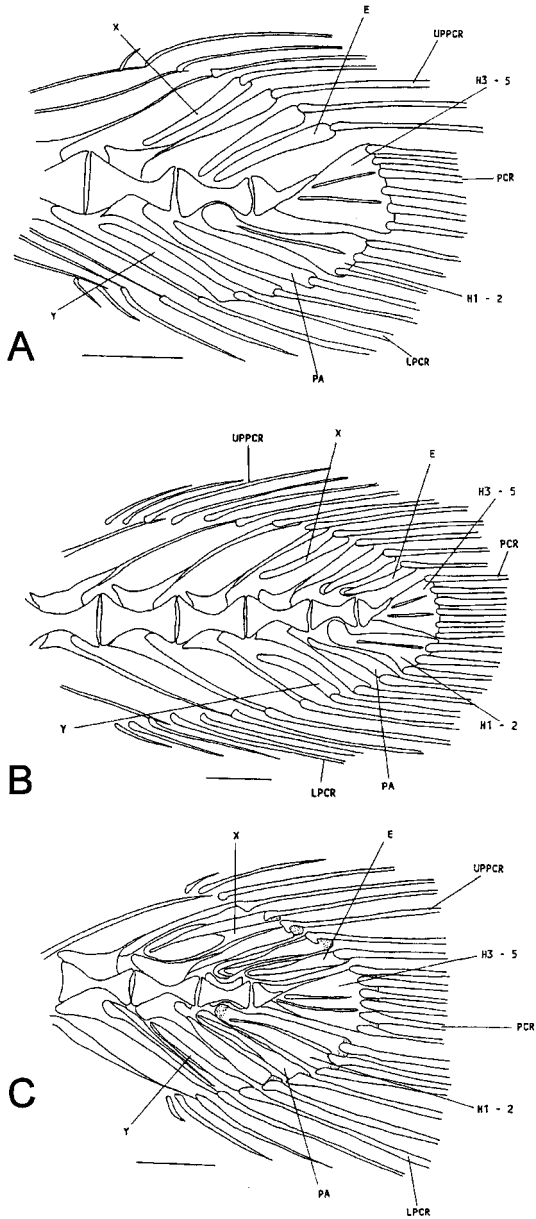

Figure 14. Left lateral view of caudal skeleton, scale = 1 mm. A. *Guttigadus globiceps* (MSU uncat.), B. *Guttigadus latifrons* (IOS 9752#1), C. *Guttigadus nana* (UMMZ 214588).

(**36**) was absent, state 1 in all *Guttigadus* except *G. nana* (Figs. 11b-d, 11f, 12c), and present, state 0 in all *Laemonema* except *L. longipes* (Figs. 11e, 12a-b). The outgroup analysis was equivocal (Figs. 12d and Table 5). The position of the foramen on the anterior blade of the hyomandibular (**37**) was below the level of the base of the opercular arm (*G. nana*), state 0 (Figs. 12c), or at the same height as the opercular arm, state 1 (Figs. 11a-f, 12a-b). The outgroup analysis was equivocal (Figs. 12d; Table 5).

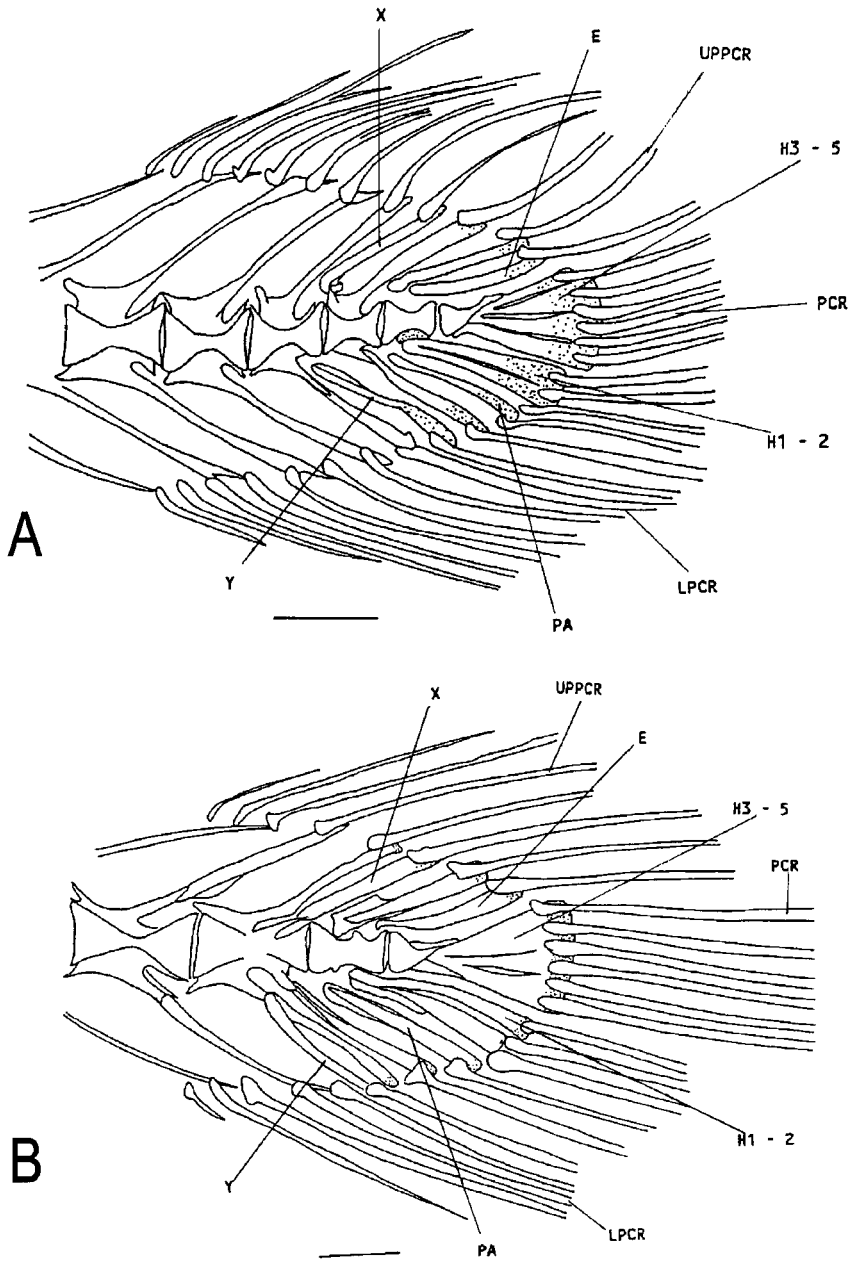

Figure 15. Left lateral view of caudal skeleton, scale = 1 mm. A. *Guttigadus nudicephalum* (MSU uncat.), B. *Physiculus fulvus* (USNM 232481).

The length of the supero-posterior blade of the hyomandibular (**38**) was either short, state 0 (Figs. 11c-f, 12b), or long, state 1 (Figs. 11b, 12a, 12c). The outgroup analysis was equivocal (Figs. 12d; Table 5). The length of the antero-inferior blade of the hyomandibular (**39**) was either short, not reaching the level of the lower articulation of the hyomandibular with the interhyal and symplectic (*L. verecundum*), state 0 (Fig. 11f) or long, reaching the

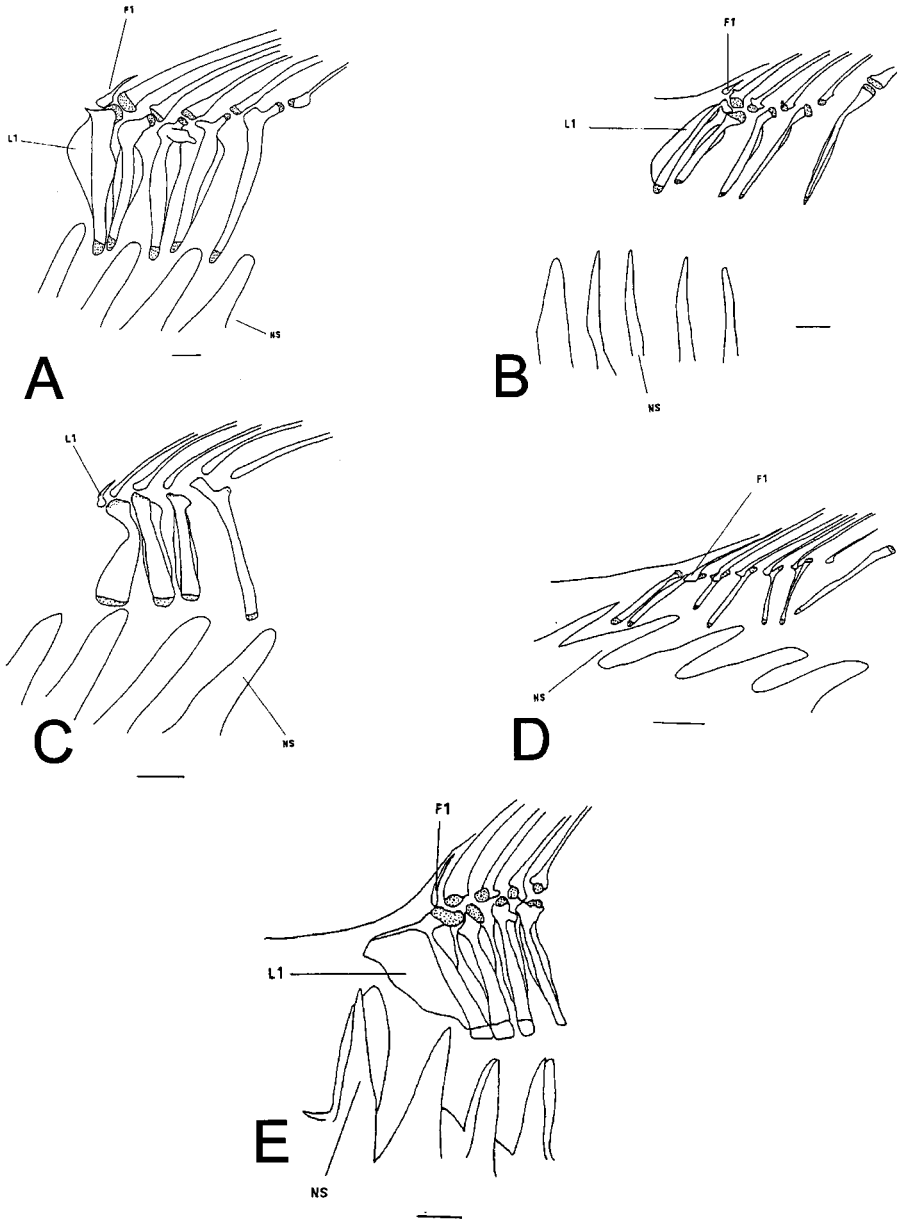

Figure 16. Left lateral view of first dorsal fin osteology, showing presence/absence of laminar bone in the first pterygiophore, scale = 1 mm. A. *Laemonema yarrelli* (MSU 16047), B. *Guttigadus globosus* (NMNZ 25203), C. *Guttigadus latifrons* (MSU uncat.), D. *Guttigadus nana* (UMMZ 214588), E. *Lepidion eques* (USNM 211787).

level of the lower articulation, state 1 (Figs. 11a-e, 12a-c). The outgroup analysis was equivocal (Figs. 12d; Table 5).

Caudal skeleton. The caudal skeleton of gadiform fishes has been well studied by Patterson and Rosen (1989) and Markle (1989) who describe the general arrangement for

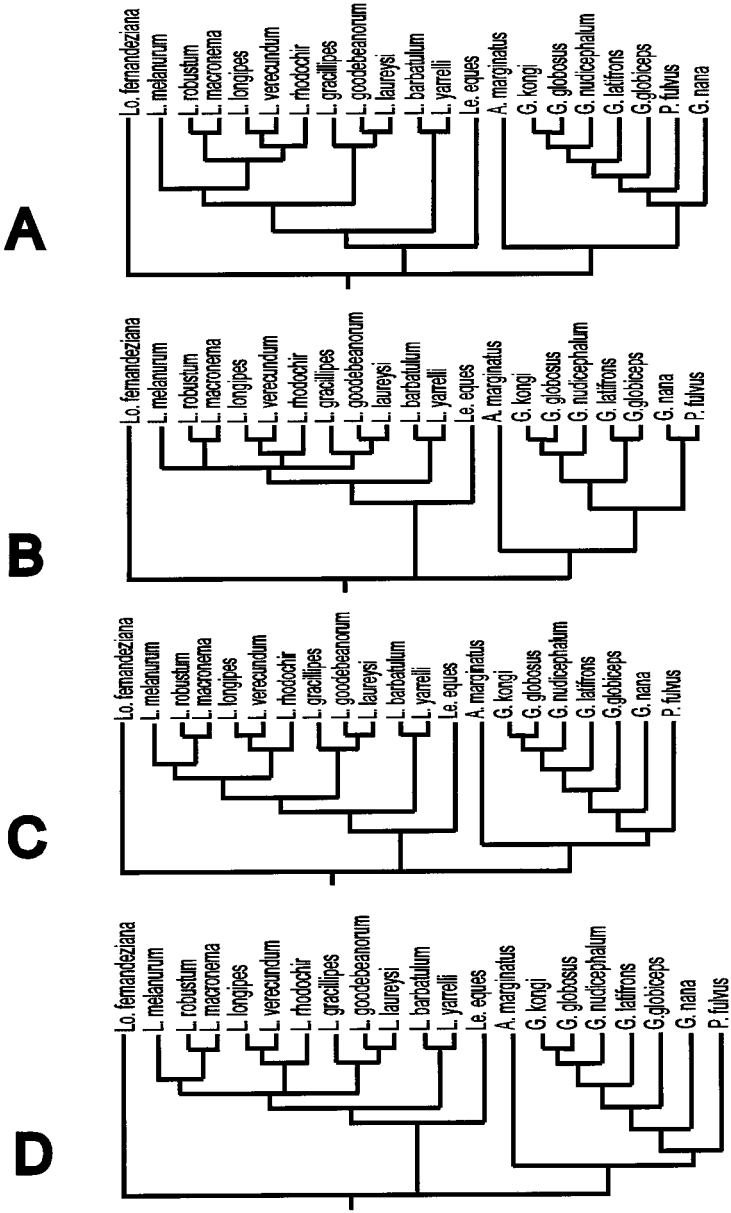

Figure 17 A-D. Four topologies for *Laemonema* and *Guttigadus* when all four outgroups are included.

a morid, such as *Euclichthys polynemus*, as two epurals, a lower autonomous hypural plate of fused hypurals 1 and 2, an upper hypural plate fused to ural centrum 2 composed of fused hypurals 3-5, one parhypural, X and Y bones. Principal or procurrent caudal rays are born on all of these structures and some procurrent rays are unsupported or supported by neural and haemal spines (Figs. 13-15).

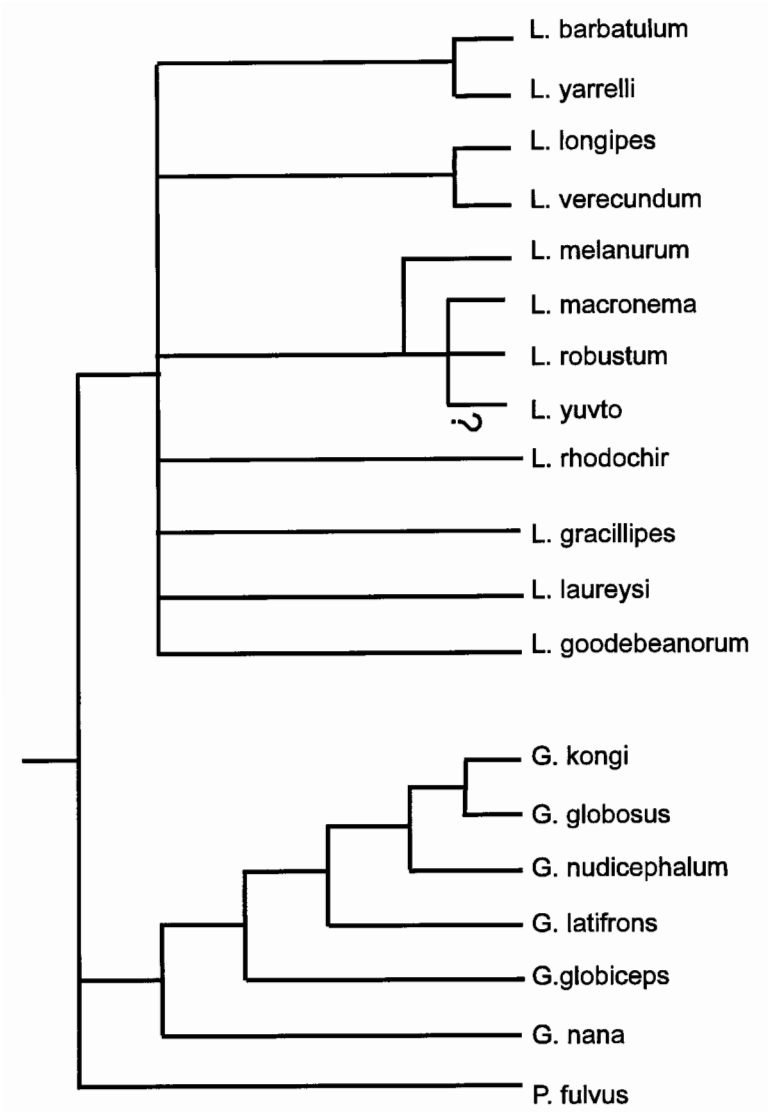

Figure 18. Preferred cladogram for *Laemonema* and *Guttigadus* with *P. fulvus* as the outgroup.

The number of upper procurrent caudal rays (**40**) was 10-14, state 0 (Figs. 13b, 14b, 15a), or 9 or less, state 1 (Figs. 13a, 13c, 14a). The outgroup was equivocal (Figs. 15b and Table 5). The number of lower procurrent caudal rays (**41**), was 16-18 in *L. barbatulum*, state 0 (Figs. 13a), or 9-15, state 1 (Figs. 13b-c, 14, 15a). The outgroup was equivocal (Figs. 15b; Table 5).

The position of the base of the anterior upper procurrent caudal ray (**42**) opposite the 2nd-4th preural vertebrae was state 0 (Figs. 13b-c, 14b, 15a), and the position opposite the first preural vertebrae was state 1 (Figs. 13a, 14a, 15c). Outgroup analysis was equivocal (Figs. 15b; Table 5). The position of the base of the anterior lower procurrent caudal ray (**43**) opposite the 3rd-5th preural vertebrae was state 0 (Figs. 13a-c, 14b, 15a), and the

position opposite the 1st-2nd preural vertebrae was state 1 (Figs. 14a, 14c). Outgroup analysis was equivocal (Figs. 15b; Table 5).

Dorsal and anal fin. The position of the anus far in front of the anal fin (**44**) was the derived state, state 1, and the position near the anal fin was the plesiomorphic state, state 0. All outgroups have state 0 (Table 5). All *Laemonema* except *L. yuvto* have the anus near the anal fin and all *Guttigadus* except for *G. nana* have the anus far from the anal fin.

Laminar bone on the first pterygiophore of the first dorsal fin (**45**) was either absent, state 0 (Figs. 16c-d), moderately developed, state 1 (Figs. 16a-b), or well developed, state 2 (Fig. 16e). Outgroup analysis was equivocal (Table 5).

The number of precaudal vertebrae anteriad of the first anal fin ray (**46**) showed two characters states, 14 or greater was state 0, and 13 or less was state 1. The outgroup analysis was equivocal (Table 5). All *Guttigadus* and some *Laemonema* had fewer than 13 while most *Laemonema* 14 or more. *G. nana* had only ten precaudal vertebrae anteriad of the first anal fin ray, the lowest value found.

The presence of a fleshy base in the vertical fins (**47**) was derived, state 1, and its absence plesiomorphic, state 0. All outgroups share the plesiomorphic state (Table 5). *Laemonema* and *G. nana* have the plesiomorphic state and all other *Guttigadus*, even juveniles as small as 57 mm (*G. kongi* NMNZ P.23396), have fleshy bases in their vertical fins.

A black stripe along the membranes of the first and second dorsal fins (**48**) was considered derived, state 1, and its absence was plesiomorphic, state 0. All outgroups have the plesiomorphic state (Table 5). The derived state is a synapomorphy of *L. barbatulum* and *L. yarrelli*.

Other characters. Adult living depths (**49**) were coded as state 0 for species living deeper than 70 m and state 1 for *G. nana* which lives shoaler than 70 m. The outgroup analysis was equivocal (Table 5).

CLADOGRAMS. —The phylogenetic analysis using all nominal outgroups, but excluding *L. yuvto*, produced 12 equally parsimonious trees of 157 steps, consistency index (CI) of 0.39 and retention index (RI) of 0.59. All trees suggest that *Laemonema* sensu lato is not monophyletic but rather contains two clades. One clade includes *Laemonema* and *Lepidion*; the other includes *Guttigadus, Physiculus, Austrophycis*, and *Lotella*. Four topologies of three trees each were found (Figs. 17). One outgroup taxon, *P. fulvus*, was usually the sister to all *Guttigadus* but sometimes formed a basal sister pair with *G. nana* (Fig. 17b) or was the second branch within *Guttigadus* after a basal *G. nana* (Fig. 17a).

Because we are uncertain of sister group relationships, we attempted to increase resolution by using each outgroup taxon (*Austrophycis marginatus, Lepidion eques, Lotella fernandeziana*, and *Physiculus fulvus*) singly. Two sister clades, *Laemonema* and *Guttigadus* were usually in each tree for each outgroup (CI's tended to be about 0.47 , RI's about 0.63 and steps about 127). Because Paulin (1989) included the "*Laemonema*" subgroup in his "*Physiculus*" group and we have two additional synapomorphies for *Physiculus*+*Laemonema* sensu lato (**39**-long antero-inferior blade of the hyomandibular, and **41**-low number (9-15) of lower procurrent caudal rays), we selected *P. fulvus* as the most likely sister taxon and best possible outgroup taxon. A 90% majority rule consensus of 82 trees produced a completely resolved *Guttigadus* and a partly resolved *Laemonema* (CI = 0.52, RI = 0.69, length = 117+). The *Guttigadus* clade was paraphyletic as *G. nana* was basal to *Guttigadus*+*Laemonema*, but tree length only increased by two steps when *G. nana* was made the basal member of *Guttigadus* (Fig. 18). We follow a conservative

approach placing *G. nana* in *Guttigadus*, based on the assumption that its neotenic features have obscured relationships. The other neotenic form, *L. verecundum*, has previously caused similar nomenclatural problems (see below). The *Laemonema* clade contains a polytomy and we are unable to confidently resolve a sister group relationship even in the very similar *L. goodebeanorum* and *L. laureysi*.

Monophyly of the ingroup, *Laemonema* sensu lato, is supported (Fig. 18) by one synapomorphy, the length of the third pelvic fin ray being less than 45% the length of the longest pelvic fin ray (**18**). This is essentially the traditional character, often described as two long pelvic rays, used to define the group. Additional characters supporting this node, but reversed in *G. nana* are: more than eight lower gill rakers (**4**), the presence of a vomer (**32**), and the position of the foramen at the same height of the opercular arm in the hyomandibular bone (**37**).

We recognize two genera, *Laemonema* and *Guttigadus*, which were consistently identified in the analyses. The monophyly of *Laemonema* (Fig. 18) is only weakly supported by one synapomorphy (**17**, two pelvic rays visible) and nine homoplasies: presence of an interarcual cartilage (**10**); first epibranchial 90-120% of length of second epibranchial (**12**); pointed cartilage of superior arm of pelvic girdle (**14**); length of third pelvic fin ray (**18**) less than 15%, absence of ligament between swimbladder and cranium (**22**), rectangular shape of maxillary process (**30**), short supero-posterior blade of hyomandibular (**38**), base of anterior lower procurrent caudal fin opposite 3rd to 5th preural vertebrae (**43**), and 14 or more precaudal vertebra anteriad of first anal fin ray (**46**).

Sister species *Laemonema longipes* and *L. verecundum* (Fig. 18) are supported by two synapomorphies, cornua not reaching skin above operculum (**23**) and absence of a posterior notch in maxillary process (**31**), and two homoplasies, absence of a neck in the swimbladder (**20**), and the v-shaped vomer (**34**).

Sister species *Laemonema barbatulum* and *L. yarrelli* (Fig. 18) are supported by one synapomorphy, presence of a black stripe in the upper portion of the first and second dorsal fin (**48**), and one homoplasy, length of hyomandibular greater than 50% of its opercular arm (35).

Sister species *L. robustum* and *L. macronema* (Fig. 18) are supported by three synapomorphies, presence of a groove on the 3rd and 4th strut of the 3rd pharyngobranchial (**13**), presence of a foramen in the pelvic girdle (16), and presence of a small neck in the swimbladder (**20**), and two homoplasies, cylindrical shape of the cornua (**24**), and more than 50 teeth on the external row of one side of the upper jaws (**29**).

Guttigadus is supported by two synapomorphies (Fig. 18), the PCA score of D2, A, PCV and CV (**2**) and the comparatively short length of the coracoid arm in the pectoral girdle (**26**), and five homoplasies, absence of uncinate process on first epibranchial (**9**), absence of interarcual ligament (**11**), five or fewer pelvic fin rays in adults (**19**), hyomandibular more than 50% longer than its opercular arm (**35**), and absence of laminar bone on the first pterygiophore of the first dorsal fin (**45**).

All *Guttigadus* above the *G. nana* node are supported by three synapomorphies, wide (7.1-15% SL) interorbital width (**1**), fewer than seven parapophyses associated with the second chamber of the swimbladder (**21**), and fleshy base of the vertical fins (**47**), and three homoplasies, highly modified scales on the lateral line (**5**), absence of an anterior lateral blade behind the body of the hyomandibular (**36**), and anus position far in front of the anal fin (**44**).

The node above *G. globiceps* (Fig. 18) is supported by one synapomorphy, the third pelvic fin ray is 15-40% the length of the largest pelvic fin rays (**18**), and three homoplasies: 10-14 upper procurrent caudal fin rays (**40**), the first preural vertebra opposite the base of the most anteriad upper procurrent caudal fin ray (**42**), and the 3rd to 5th preural vertebrae opposite the most anteriad ray of the lower procurrent caudal ray (**43**). The node above *Guttigadus latifrons* is supported by two homoplasies, an angle equal to or greater than 90° between superior and inferior pelvic arms (**15**), and the presence of a medium size laminar bone on the first pterygiophore of the first dorsal fin (**45**). The sister species *G. globosus* and *G. kongi* are supported by two homoplasies, presence of an interarcual ligament (**11**), and presence of a short supero-posterior blade of the hyomandibular bone (**38**).

This cladogram (Fig. 18) supports Rass's (1954) general idea of interrelationships of *Laemonema* sensu lato. Rass (1954) distinguished two groups, equivalent to *Laemonema* and *Guttigadus* as recognized here. In fact, one of his characters, the wide interorbital width, is a synapomorphy of all *Guttigadus*, except *G. nana*, and is the most easily recognized feature of the genus. *Guttigadus*, as defined herein, includes four species removed from *Laemonema* (*G. globiceps*, *G. kongi*, *G. latifrons*, and *G. nana*); it is supported by two synapomorphies and is relatively well resolved. *Guttigadus nana* is the most atypical member and appears to be paedomorphic with neotenic characteristics.

KEY TO ADULT *LAEMONEMA* AND *GUTTIGADUS*

(n = number of individuals).

1a.- Interorbital width 7.1-15 % SL 2
1b.- Interorbital width 3.0-7.0 % SL 6
2a.- Gill rakers on lower limb of first gill arch 22-30 (n = 46) ..... *G. globiceps*
(Chile, Argentina, South Africa, Australia, New Zealand)
2b.- Gill rakers on lower limb of first gill arch less than 22 3
3a.- Gill rakers on upper limb of first gill arch 3-5 (n = 5) ..... *G. nudicephalum*
(Eastern South Africa)
3b.- More than 5 upper gill rakers on first arch 4
4a.- Gill chamber, floor of mouth, and lips pale (n = 50) ..... *G. kongi*
(Chile, Argentina, Southern Ocean, Australia, New Zealand)
4b.- Gill chamber, floor of mouth, and lips dark 5
5a.- Lower jaw included in upper jaw; scales on a straight line 111-137; scales below lateral line 27; lower gill rakers 17-22 (n = 10) ..... *G. globosus*
(New Zealand, subtropical South Atlantic)
5b.- Lower jaw not included in upper jaws; scales on a straight line 145-150; scales below lateral line 38; lower gill rakers 14-17 (n = 22) ..... *G. latifrons*
(north-eastern Atlantic, south-western Indian Ocean)
6a.- Upper gill rakers 1-2; caudal vertebrae 27-30 (n = 11) ..... *G. nana*
(Japan)
6b.- Upper gill rakers more than 2; caudal vertebrae 29-43 7
7a.- P1 with 16-24 rays 8
7b.- P1 with 25-31 rays 15
8a.- Caudal vertebrae 29-31, D1 with 8-9 rays (n = 3), caudal peduncle elongate and thin, its depth 12-15% of length ..... *L. verecundum*
(eastern central Pacific)
8b.- Caudal vertebrae 34-43, D1 with less than 8 rays, caudal peduncle shorter, its depth usually more than 20% of length 9

9a.- P1 16-18, barbel absent (n = 12) ..... *L. longipes*
(north-western Pacific, Bering Sea)
9b.- P1 more than 18, barbel present 10
10a.- Scales on a straight line 150-172 (n = 5) ..... *L. gracillipes*
(tropical eastern Pacific)
10b.- Scales on a straight line less than 150 11
11a.- Lower gill rakers 10-13 12
11b.- Lower gill rakers greater than 13 13
12a.- Lower procurrent caudal fin rays 14-20, second fin ray of D1 elongated and black in adults; scales on a straight line 128-140 (n = 79) ..... *L. barbatulum*
(tropical and subtropical western North Atlantic)
12b.- Lower procurrent caudal fin ray 11-13, second fin ray of D1 not elongated and brown in adults; scales on a straight line 105-130 (n = 20) ..... *L. rhodochir*
(Kyushu-Palau Ridge, Hawaii, Sala y Gomez Ridge)
13a.- Upper portion of D1 and D2 with a black stripe (n = 22) ..... *L. yarrelli*
(subtropical North Atlantic)
13b.- Upper portion of the D1 and D2 without a black stripe 14
14a.- D2 rays 63-72 (mode = 66); A rays 60-69 (mode = 64); total vertebrae 53 -58 (mode = 55) (n = 44) ..... *L. laureysi*
(subtropical and tropical eastern Atlantic)
14b.- D2 rays 66-73 (mode = 70); A 65-71 rays (mode = 67); total vertebrae with 56-59 (mode = 57) (n = 5 0) ..... *L. goodebeanorum*
(subtropical and tropical western Atlantic)
15a.- P1 rays 31, highly modified scales on lateral line (n = 1) ..... *L. yuvto*
(Sala y Gomez Ridge)
15b.- P1 rays less than 31, no highly modified scales on lateral line 16
16a.- P2 rays more than 49 % SL, (n = 3) ..... *L. macronema*
(western Indian Ocean)
16b.- P2 rays less than 49 % SL 17
17a.- D1 rays 7; a triangular black spot on posterior tips of D2 and A, a vertical black band on caudal fin (n = 18) ..... *L. melanurum*
(western North Atlantic)
17b.- D1 rays less than 7; no triangular black spot on posterior tips of D2 and A, a vertical black band on the caudal fin ..... *L. robustum*
(tropical eastern Atlantic, North Pacific and South western Pacific).

Taxonomic Accounts

Laemonema Günther in Johnson, 1862

Laemonema Günther in Johnson, 1862:171 (type species *Laemonema robustum* Johnson, 1862 by monotypy).
Microlepidium Garman 1899 (type species *Microlepidium verecundum* (Jordan and Cramer *in* Gilbert, 1897) by subsequent designation of Jordan).
Laemonemodes Gilchrist, 1903:208 (type species *Laemonemodes compressicauda* Gilchrist, 1903 by monotypy).
?*Gargilius* Jensen, fide Schmidt, 1906 *in* Holt and Byrne,
1908b (nomen nudum)
?*Gargilius* Jensen in Koefoed, 1953:11 (type species *Gargilius lucullus* Jensen, 1953 by subsequent designation of Cohen, 1973).
?*Svetovidovia* Cohen, 1973 *in* Hureau and Monod 1973:326 (replacement name for *Gargilius*)
?Svetovidovia: Fahay and Markle, 1984:265-272. Cohen, 1986:723. Markle, 1989:83. Paulin, 1989:248.
Lepidion (not of Swainson): Haedrich, 1964: 15 (juvenile reference for *L. barbatulum*).

Diagnosis. —A morid with interorbital width equal to or shorter than orbit diameter; six to nine rays in first dorsal fin, with first dorsal ray almost always beneath skin; second dorsal fin with 40-73 rays; anal fin with 41-71 rays; teeth on vomer; caudal peduncle small and thin; chin barbel usually present; adults with two well-developed pelvic rays and two to nine small inner rays under the skin; photophores absent; known juveniles without numerous vertical bars on sides.

Comments. —On 8 November 1862, Günther erected *Laemonema* for *Phycis yarrelli* Lowe, but on 10 June 1862, Johnson published a paper which referred to *Laemonema* Günther MS and described a new species *L. robustum* (D. M. Cohen pers. comm., 1989). The genus name should be attributed to Günther (in Johnson 1862) with the type species as *Laemonema robustum* Johnson, 1862 (Eschmeyer, 1990).

Cohen (1986) erected *Svetovidovia* to accommodate a preoccupied *Gargilius* Jensen. It is characterized by the presence of seven or more pelvic fin rays, a feature that apparently led Haedrich (1964) to consider *Svetovidovia* to be juveniles of *Lepidion*. But, *S. vitellius* was tentatively referred to the juvenile stage of *Laemonema* by Fahay and Markle (1984), based on a transitional specimen showing ontogenetic loss of pelvic fin rays. They did not assign *S. vitellius* to any known species of *Laemonema*.

Three grade groups of *Laemonema* can be distinguished based on a principal components analysis of selected meristics: D2, A, PCV, P1, LGR and UGR (Fig. 19). One group, *L. barbatulum, L. macronema, L. melanurum, L. robustum, L. rhodochir,* and (presumably) *L. yuvto*, is characterized by a comparatively higher number of rays in P1, lower number of rays in D2 and A, and a lower number of PCV, UGR and LGR. A second group, *L. gracillipes, L. longipes, L. goodebeanorum, L. laureysi,* and *L. yarrelli*, is characterized by values opposite the first group. A third monotypic group, *L. verecundum*, is characterized by the lowest values for D2, A, and PCV (Table 4). Most, but not all members of the first group, those with fewer D2 and A rays, also have high first dorsal fins (Fig. 21). Three of the five in the second group have low first dorsal fins.

In the following we present species accounts on the basis of the grade groupings, but show distributional information based on clades. In part this is because some features of the grade groups, such as long D2 and A, lend an overall similarity to members of the grade.

Laemonema barbatulum Goode and Bean, 1883

Figure 21a

Laemonema barbatulum Goode and Bean, 1883:204-206.
Laemonema barbatula: Goode and Bean, 1896:362-363. Garman, 1899:188. Parin, 1984:57.
Gargilius vitellius Koefoed, 1953:11.
Lotella maxillaris Bean, 1884:241.

Diagnosis. —Body low and slender, covered by small deciduous scales. Gill rakers 3-6+10-13, total = 14-18. Caudal fin with 7-9+6+14-20 rays. Tips of dorsal and anal fins edged in black.

Description. —Head 18.8-26.7 % SL, mouth subterminal. Snout short, 4.5-8.2% SL. Maxillary with an external row of conspicuous canine-like teeth and two or three rows of small villiform teeth. Dentary with two rows of canine-like teeth, external teeth larger than internal teeth. Teeth on vomer canine-like, in a rounded patch. Chin barbel 1.3-5.0% SL., smaller than orbit diameter. Orbit diameter 5.2-8.9% SL, at least three times in

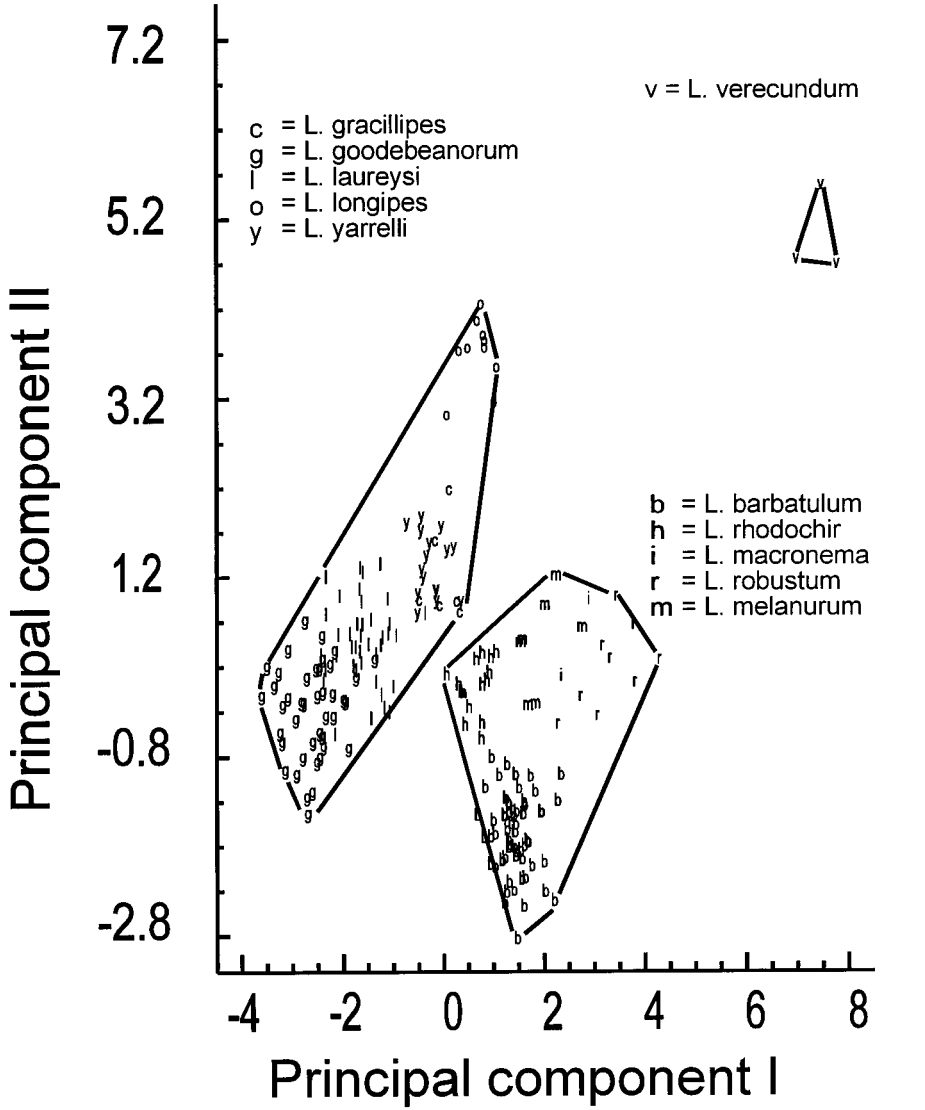

Figure 19. Principal component analysis using PCV, CV, D2 and A for *Laemonema*, except *Laemonema yuvto*.

head length. Interorbital narrow 3.9-6.1% SL, almost four times in head length and almost twice in orbit diameter. Maxillary 7.7-12.7% SL, ending about same level as the posterior end of pupil. Opercle bone ending in a flat spine in its upper portion. Postorbital length 8.2-11.1% SL.

Greatest depth of body near anus, 13.8-38.1% SL; depth at first anal ray 13.2-28.4% SL. Anus and anal fin separated by a short distance, smaller than height of caudal peduncle. Preanus length 32.7-57.0% SL. Preanal fin length 35.0-56.5% SL. Predorsal length 22.1-28.9% SL. Depth at anus 11.1-25.4% SL. Caudal peduncle depth 1.7-3.6% SL.

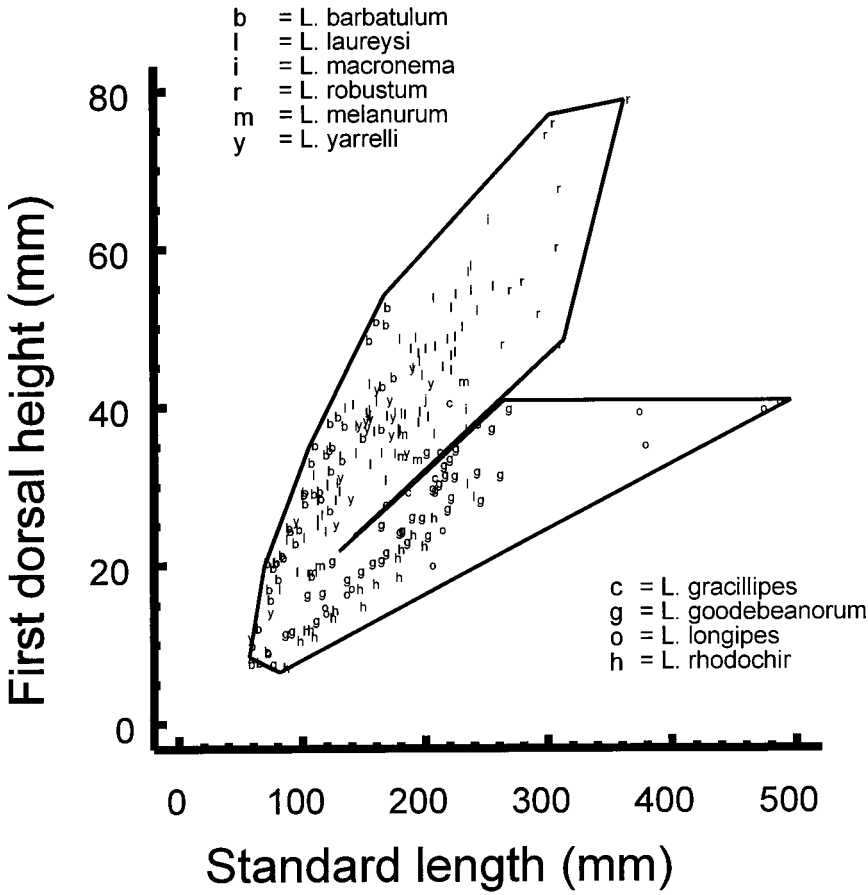

Figure 20. Relationship between first dorsal fin height (mm) and standard length (mm) in ten species of *Laemonema.*

First dorsal fin rays 6, except one individual with 7; base short 3.6-5.6% SL. First ray beneath skin; second dorsal ray largest, 4.6-31.9% SL, longer than head length in well-preserved specimens, remaining rays gradually decrease in length. Second dorsal fin rays 57-63, with large base 56.6-70.8% SL, ray lengths gradually decrease from origin to insertion. Anal fin rays 54-63, shorter than second dorsal fin 43.5-61.9% SL. Pectoral fin rays 19-23, prepectoral length 21.3-31.4% SL, its base 2.9-5.6% SL. In adults pelvic fin with two elongated rays; its length 6.9-37.0% SL, not reaching vent; 2-3 small pelvic rays below the skin. Caudal fin asymmetrical, lower procurrent caudal fin rays 14-20, upper procurrent rays 7-9, principal rays 6. Total vertebrae 50-56, precaudal 13-15, caudal 37-42. Gill rakers 3-6+10-13, total = 14-18. Lateral line not well defined, on a straight line about 128-140 scales. Scales above lateral line 12-15, scales below lateral line 21-30.

Comparisons. —*Laemonema barbatulum* is very similar to *L. yarrelli* but has fewer lower gill rakers (10-13 vs 14-18), more lower procurrent caudal rays (14-20 vs 10-12), and more scales on a straight line (128-140 vs 100-111). *Laemonema barbatulum* is also

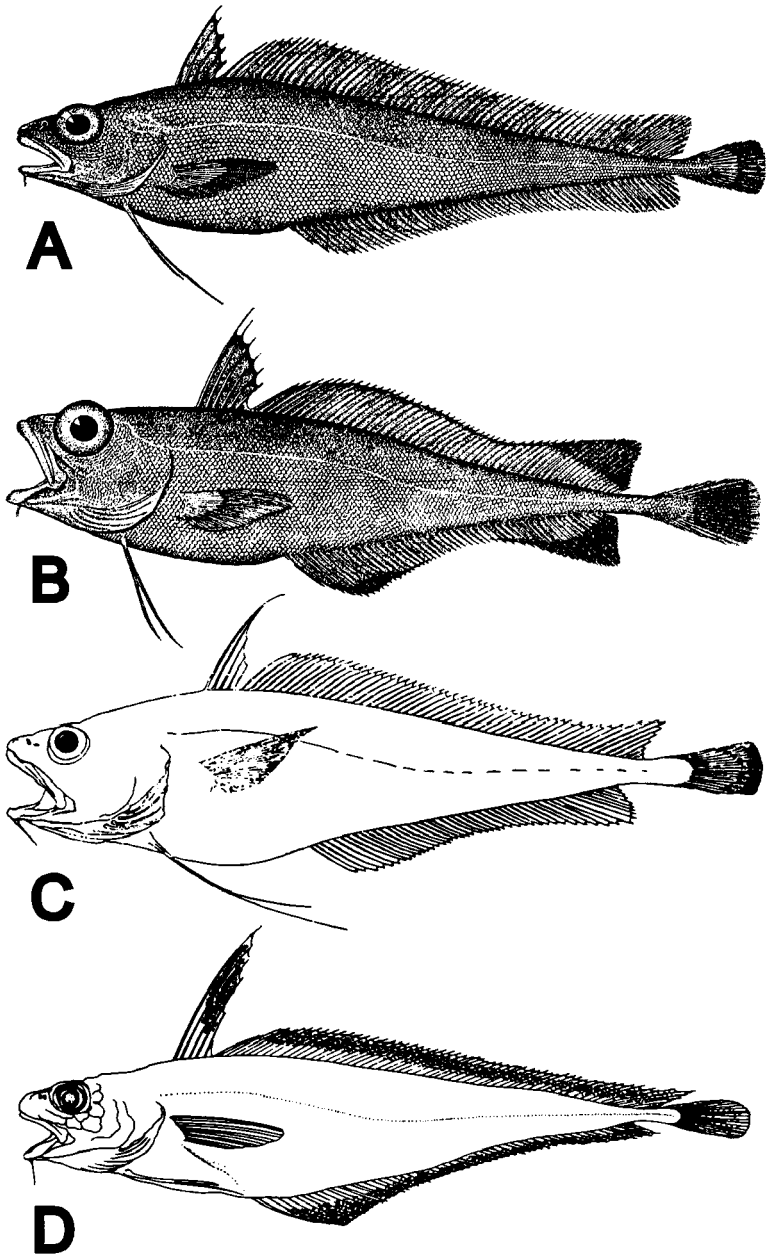

Figure 21. A. *Laemonema barbatulum*, from Goode and Bean, 1896, fig. 315; B. *Laemonema melanurum*, from Goode and Bean, 1896, fig. 316; C. *Laemonema robustum*, from Cohen, 1986; and D. *Laemonema yarrelli*, from Cohen, 1986.

similar to *L. rhodochir* but has more lower procurrent caudal fin rays (14-20 vs 11-13), a black stripe on the vertical fins, and an interarcual ligament which is not found in *L. rhodochir*. *Laemonema barbatulum* differs from *L. robustum* in having fewer scales below lateral line (21-30 vs 39-47), fewer upper procurrent caudal fin rays (7-9 vs 10-12), a

"neck" between the two chambers of the swimbladder (the "neck" is absent in *L. robustum*), and a black stripe on the vertical fins. *Laemonema barbatulum* differs from *L. macronema*, mainly in having fewer pectoral fin rays (19-23 vs 27), smaller pelvic fin rays (6.9-37.0% SL vs 49.0-65.0%), and a "neck" between the two chambers of the swimbladder. *Laemonema barbatulum* differs from *L. melanurum* in having fewer pectoral fin rays (19-23 vs 25-27), fewer scales above lateral line (12-15 vs 18), and fewer scales below lateral line (21-30 vs 35-36). It also lacks the triangular black patches on the upper end of the dorsal and anal fins, and rectangular black patch on the caudal fin found in *L. melanurum*. *Laemonema barbatulum* differs from *L. yuvto* in having fewer pectoral fin rays (19-23 vs 31), no modified scales on lateral line, and black stripes on the vertical fins.

Color in alcohol. —This species has a yellowish to light brown body, dorsal and anal fins have a narrow black line along contours; second ray of first dorsal fin black.

Juveniles. —Koefoed (1953) described *Gargilius vitellius* with the following meristic data: D1 5, D2 63, A 62, P1 17(r), 18(l), P2 10, and caudal rays 28 (7+9+12). Our counts from a radiograph of the holotype (ZMB 4471, 47.9 mm SL) showed the following: D1 6, D2 61, A 58, PCV 14, CV 40, TV 54, caudal rays 7+6+16, and counts from the specimen: P1 21, P2 11, GR 12+5. Except for pelvic counts, these data are within the range of *L. barbatulum* (Table 4) and outside the range of other species in the North Atlantic (*L. goodebeanorum* has higher and *L. robustum* lower vertical finray counts, *L. melanurum* has higher pectoral ray counts, and *L. yarrelli* has higher gillraker counts). We believe Koefoed's specimen is a juvenile *L. barbatulum*.

Cohen (1979, and pers. comm., 1989) stated that *Lotella maxillaris* Bean, 1884 from the western North Atlantic, was probably a juvenile *Laemonema*. A radiograph of the holotype of *L. maxillaris* (USNM 29832, ca. 58.0 mm SL, head damaged) revealed the following: D1 6, D2 61, A 58, PCV 14, CV 40, TV 54; and from direct examination: P1 22, P2 10, CR 8+6+16. Again, the meristic data agree with *L. barbatulum*.

We have been unable to locate the type of *G. lucullus* in the presumed repositories (ZMUC or ZMB, Nielsen, pers. comm., 1989; Byrkjedal, pers. comm., 1989). Koefoed (1953) described differences in pelvic fin and anal fin position relative to *G. vitellius*, but we can not resolve its identity, including the possibility that it could be *Guttigadus*.

Pelagic juveniles of *L. barbatulum* were illustrated by Koefoed (1953), Fahay and Markle (1984, fig. 138c,d), and Markle (1989, fig. 18). The largest from Fahay and Markle (1984) is typical of most specimens (Fig. 22). A band of pigment on the caudal peduncle, extending onto the vertical fins in larger specimens, may have been Koefoed's (1953) "indications of dark transverse bands." Alternatively, he may have been referring to specimens of *L. goodebeanorum* (see below). A band of pigmentation and the more anteriad insertion of the pelvics were useful features in distinguishing the series from *L. melanurum* (Fig. 22). In some larger specimens, all meristic values agree with *L. barbatulum* (64.8 mm, MCZ 59773) while in others (66 mm, MCZ 86752) there may be five larger and five smaller pelvic fin rays. The ontogenetic reduction of pelvic rays begins around 60 mm and most smaller fish have 10-11 pelvic fin rays (Fig. 23). This reduction in pelvic fin ray number is presumed associated with metamorphosis and is also associated with a distended gut or glutinous feeding stage (Markle 1989).

The smallest individual of *L. barbatulum* examined was 7.45 mm NL pre-flexion larva (NMFS, Sandy Hook Lab, A16 85-02 st 26 6B5). The head (33.0% NL) and eyes (9.66% NL) were large. The deepest part of the body is near the insertion of the pelvic fins (Fahay and Markle, 1984, fig. 138c). Dorsal, anal and pectoral fins have the adult comple-

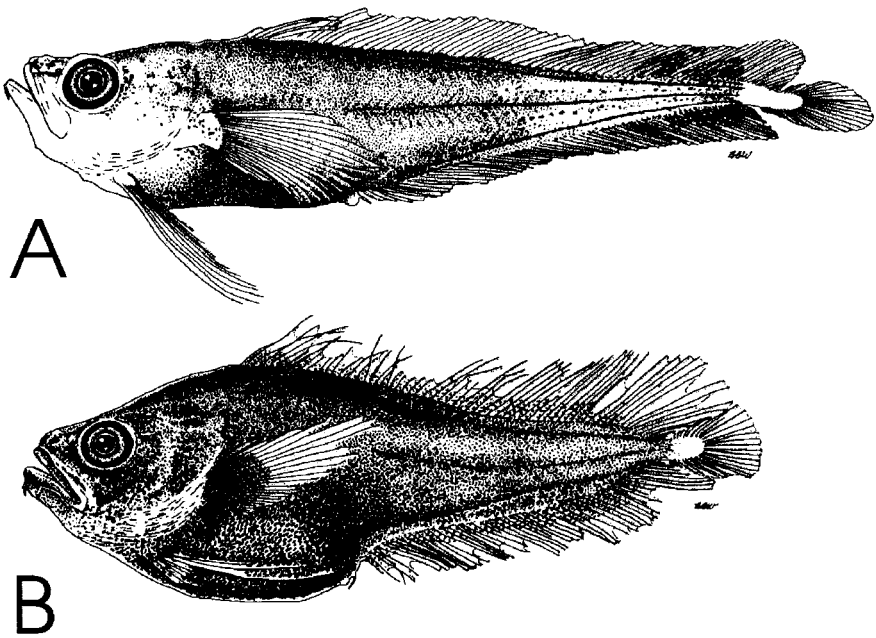

Figure 22. Pelagic juvenile stage. A. *Laemonema barbatulum*, 44.4 mm SL, ARC H6901 and B. *Laemonema melanurum*, 44.1 mm SL, ARC H9455, reproduced from Fahay and Markle (1984) with permission.

ments and pelvic fins have 10 rays. Caudal rays appear to be the last to form and all fins are formed by at least 25 mm. Gill rakers are completely developed in specimens above 11 mm SL. There are two unpigmented areas on the trunk, one midway along the vertical fins and another in the caudal peduncle. Both areas persist through development. Three lateral, dark-brown horizontal lines are found on the dorsal, mid-lateral, and ventral areas of the posterior 1/3 of the body, but not reaching the caudal peduncle. These blend into the overall diffuse body pigmentation with growth. The body pigmentation is heaviest on and above the viscera and lightest on the head. The posterior band separating the two unpigmented areas begins to spread onto the dorsal and anal fins around 25 mm.

Distribution. —Laemonema barbatulum is found on continental slopes in the temperate and tropical western North Atlantic, from 40° 17' N, 50° 39' W to 02° 37'S, 41° 03'W, over a depth of 50-1620 m (Fig. 24).

Material examined. —ARC 8602169, ARC 8707094, ARC 8707128, ARC 8706054, CAS 66824, MCZ 85890, MCZ 85891, MCZ 85905, MCZ 38310, UF 12934, UF 13120, UF 37729, UF 41031, USNM 155735, USNM 29045, VIMS 6293, ZMB 4471(holotype of *Gargilius vitellius*).

Other material of *L. barbatulum* examined but not included in analysis are deposited at MCZ (36 spec.), CAS-SU (2 spec.), UF (85 spec.), USNM (133 spec.), VIMS (2 spec.).

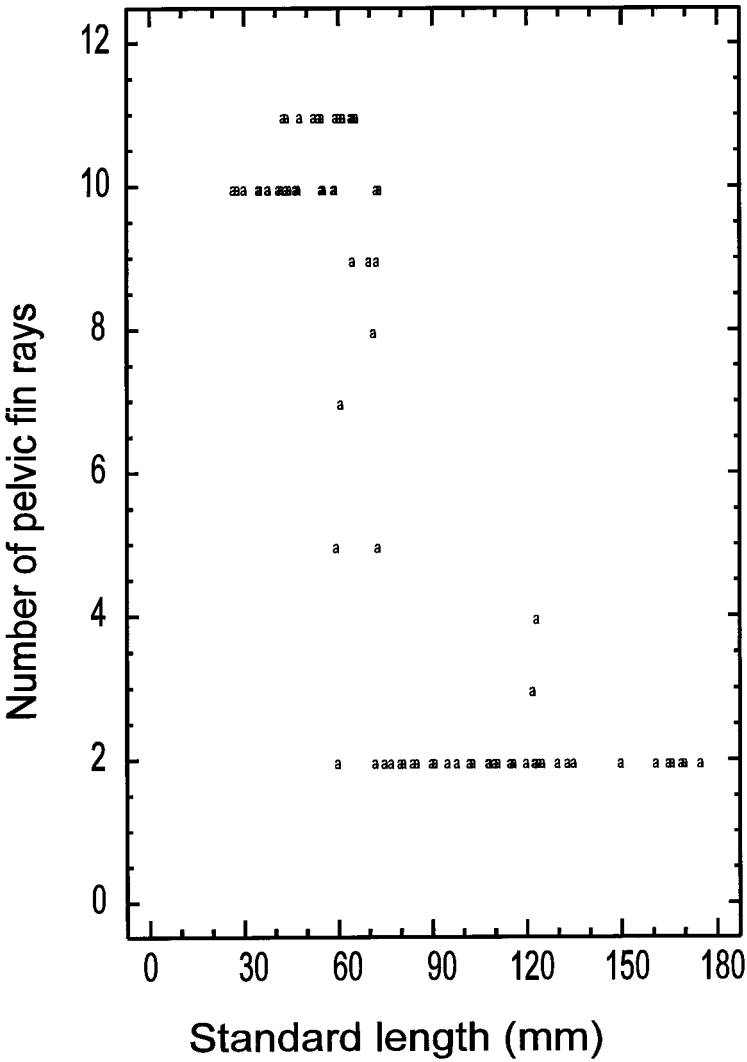

Figure 23. Relationship between pelvic fin rays and standard length for *Laemonema barbatulum*.

Laemonema melanurum Goode and Bean, 1896
Figure 21b

Laemonema melanurum Goode and Bean, 1896:363-364.
Laemonema melanurum: Holt and Byrne, 1908a: 87. Matsubara, 1938:62. Taki,1953: 208. Rass,1954:8. Lindberg and Legeza, 1965: 230. Parin,1984:57. Cohen et al. 1990: 361.

Diagnosis. —Body slightly broad, covered by small, deciduous scales; first dorsal fin with seven rays; pectoral fin with 25 -27 rays; anal fin with a conspicuous depression at middle-length; posterior end of dorsal and anal fins have a black triangle, and end of caudal fin with a black vertical band.

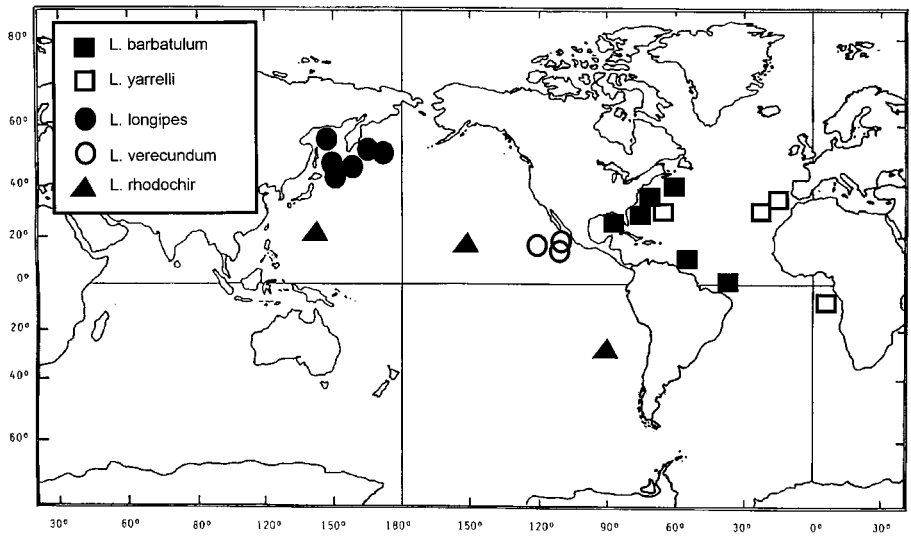

Figure 24. Species distribution chart of selected *Laemonema*.

Description. —Head length 24.4-33.2% SL; maxillary 11.2-15.9% SL, reaching middle of pupil, with outer row of strong canine-like teeth, followed by three or more irregularly distributed, small inner canine-like teeth; toothless space at symphysis. Vomer with caniniform teeth in rounded patch. Dentary with teeth arrangement similar to that of maxilla but without toothless space. Orbit diameter 7.1-11.1% SL, larger than interorbital width, 4.5-9.7% SL. Two nostrils, both near eyes, the farthest from eye with a siphon like structure, nearest with an elevated membrane. Snout short, 5.6-7.9% SL. Barbel always present, 1.8-6.4% SL. Postorbital length 10.7-13.0% SL. Opercle with a flat spine.

Predorsal length 24.4-39.2% SL, slightly greater than head length. Prepectoral length, 23.8-29.7% SL; pectoral origin about at the same vertical as origin of first dorsal fin. Prepelvic length 17.3-23.8 % SL. No separation between anus and anal fin. Preanus length 38.0-52.0% SL; preanal length 41.0-55.0% SL. Maximum depth below first dorsal fin 19.0-33.0% SL. Depth at anus 12.4-50.8% SL. Body continuously decreasing in size to caudal peduncle, which is short 1.8-3.3% SL.

First dorsal fin with seven rays, its base short, 4.7-10.9% SL, second ray longest 17.4-25.9% SL. Second dorsal fin with 53-61 rays, its base 51.2-64.1% SL. Anal fin with 52-59 rays, its base 42.5-52.4% SL. Pectoral fin with 25-27 rays, its base 3.9-7.7% SL, its length 15.8-25.0% SL. Pelvic fin with two rays, its length 17.4-30.8 % SL. Caudal fin asymmetrical, upper procurrent rays 7-10, principal rays six, lower procurrent ray 11-15. Total vertebrae 53-57, precaudal vertebrae 15-16, caudal vertebrae 38-42. Gill rakers 4-6+12-15, total = 16-21. Scales on a straight line 145-166, scales above lateral line 18, scales below 35-36.

Comparisons. —Adult specimens are not well represented in museums and we examined only six. *Laemonema melanurum* is most readily recognized by the pigmentation at the posterior ends of the dorsal and anal fins and on the caudal (Fig. 21b). *Laemonema melanurum* differs from *L. gracillipes* in having more pectoral fin rays (25-27 vs. 21-23)

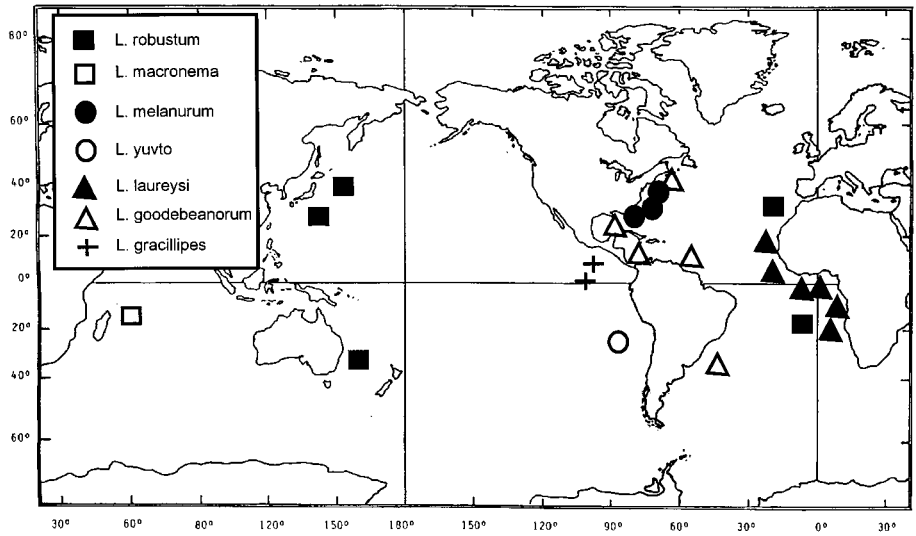

Figure 25. Species distribution chart of selected *Laemonema*.

and fewer lower gill rakers (12-15 vs. 16-21); from *L. robustum* in having more total vertebrae (53-57 vs 47-52) and fewer scales below the lateral line (35-36 vs 39-47); from *L. rhodochir* in having more pectoral fin rays (25-27 vs 22-24), more scales on a straight line (145-166 vs 105-130), and more scales below the lateral line (35-36 vs 21); from *L. yuvto* in having fewer pectoral fin rays (25-27 vs 31), more caudal vertebrae (53-57 vs 51), and more scales on a straight line (145-166 vs 135).

Color in alcohol. —Body light brown, with a prominent black patch on most of caudal fin; black patches present also at end of second dorsal and anal fins, both have thin black line along the margins.

Juveniles. —The pelagic juvenile stage (Fig. 22b) is somewhat deeper bodied than *L. barbatulum* and more densely pigmented. Both share an unpigmented caudal base (Fig. 22). The pelvic origin is at the level of the posterior margin of the preopercle rather than anteriad of the margin as in *L. barbatulum*. The ontogenetic resorption and reduction of pelvic rays appears to occur at about the same size as *L. barbatulum*. Specimens less than 50 mm have seven to 10 rays and those greater than about 100 mm have two. We have no intermediate sizes.

The smallest *L. melanurum* (15.6 mm, ARC 8707565) had all fins formed and eight rays in the pelvic fin. Area of viscera densely pigmented and caudal peduncle unpigmented. Body color light brown; two pigmented lines immediately below dorsal fin and above anal fin; head whitish except above eyes, with small melanophores arranged in rows. Maximum body depth located at origin of first dorsal fin; eyes large (38.8 % HL). In specimens 16-42 mm (ARC 8707565, ARC 8707593, ARC four specimens not catalogued, and MCZ uncat.) body pigmentation variable but generally uniformly dark.

Distribution. —This species appears restricted to continental slopes in the western North Atlantic (Fig. 25) at depths of 452-644 m.

Material examined. —Holotype - USNM 38270; others - ARC 8707565, ARC 8707577, ARC 8707593, CAS-SU 9445, USNM 38269, USNM 53058, USNM 304411.

Laemonema robustum Johnson, 1862
Figure 21c

Laemonema robustum Johnson, 1862: 167-180.
Laemonema robustum: Gúnther, 1862:357-358. Johnson, 1863: 62-64 (description). Goode and Bean, 1896: 362. Holt and Byrne, 1908a: 87. Matsubara, 1938: 62. Taki, 1953: 208. Rass, 1954: 8, Parin, 1984: 57. Cohen, 1986: 717. Edwards and Glass, 1987: 630-631. Biscoito and Maul, 1989: 2-3. Parin and Sazonov, 1990: 6-8. Cohen et al., 1990: 361.
Laemonema robustum (not of Johnson): Vaillant, 1888: 286.
Laemonema filodorsale Okamura,1982: 132-135 p.
Laemonema filodorsale: Parin,1984:57. Okamura, 1984:92. Parin and Sazonov, 1990:6. Cohen et al., 1990:361.
Haloporphyreus modestum Franz, 1910:28-29.
Laemonema modestum (Franz): Nakaya et al, 1980:41. Okamura,1984: 92. Cohen et al.,1990:361.
Laemonema sp.: Fourmanoir and Rivaton, 1979, Parin, 1984:57.

Diagnosis. —Body robust and deep 21.9-27.7% SL, with deciduous scales; pectoral fin with 26-30 rays; scales below lateral line 39-47.

Description. —Head length 24.9-29.9% SL; mouth large, almost terminal. Maxillary 12.4-14.8% SL, reaching middle to end of orbit, with external row of strong caniniform teeth, followed by at least seven rows of smaller canine like teeth; a gap at symphysis. Vomer with caniniform teeth on a rounded patch. Dentary with outer row of strong canine-like teeth, followed by two or three rows of small teeth; a small gap at dentary symphysis. Snout without scales, short 6.9-8.4% SL, with two nostril widely separated from eyes. Orbit diameter short, 5.3-7.3% SL, wider than interorbital width, 4.7-6.1% SL. Barbel 3.1-5.7% SL. Postorbital length 12.1-16.3% SL.

Predorsal fin length 27.2-32.6% SL, about equal to prepectoral length 28.2-31.6% SL. Prepelvic fin length 20.6-26.4, shorter than two previous measurements. Preanus length 38.9-45.0% SL, less than preanal fin length, 41.9-50.0% SL. Maximum depth of body 21.9-27.7% SL; depth at anus 21.7-27.5% SL, depth at first anal fin ray 21.0-27.6% SL. Body declines in depth to caudal peduncle, 2.4-3.5% SL, which is larger than barbel.

First dorsal fin with six rays its base 3.5-5.1% SL, second ray longest 15.4-25.9% SL, reaching at least first 10 rays of second dorsal fin; first ray very short and not visible (4-5 first dorsal rays reported by Okamura, 1982, do not include small first ray). Second dorsal fin with 50-57 rays, its base 55.5-66.9% SL, ray lengths decrease with decreasing body depth. Anal fin with 48-54 rays (low of 46 in Cohen 1986), its base 45.4-52.7% SL; ray lengths decrease with body depth. Pectoral fin with 26-30 rays, its base 3.5-5.4% SL, its length 17.9-21.7% SL. Pelvic fin with two rays, reaching at least fourth anal ray, its length 19.8-35.2% SL. Caudal fin asymmetrical, lower procurrent rays 12-17, principal rays 6, upper procurrent rays 10-12. Total vertebrae 47-52, precaudal vertebrae 13-15, caudal vertebrae 34-38. Gill rakers 4-7+13-16 = 17-22. Scales on a straight line 120-150, scales above lateral line 14-19, scales below lateral line 39-47.

Comparisons. —Okamura's (1982) *L. filodorsale* from Kyushu-Palau Ridge south of Japan and Franz's (1910) *L. modestum* from Yokohama, Japan, seem to refer to the same form. Unfortunately, the type of *L. modestum* was destroyed in Munich, Germany during World War II (Karrer, 1989; pers. comm.). Okamura's diagnostic features seemed to

Table 6. Comparison of selected meristic characters for *Laemonema robustum* from Atlantic Ocean and western Pacific Ocean. Values for *L. filodorsale* paratype (BSKU 29532) shown with asterisk (*), those for holotype of *L. modestum* shown with plus sign (+).

	D2								A							
	50	51	52	53	54	55	56	57	47	48	49	50	51	52	53	54
Atlantic Ocean	1		2	2	1		1			1	1	3	1		1	
Japan and Kyushu Palau Ridge	1+		1		1	4*	1	1	1+	1	2	2*	3			
Australia and New Caledonia						1		1						1		1

	PCVERT			CVERT					P1				
	13	14	15	34	35	36	37	38	26	27	28	29	30
Atlantic Ocean	5	1		1		2	2	1		2	2	3	
Japan and Kyushu Palau Ridge		3*		1	1	1*			1*	1	4		1
Australia and New Caledonia		1	1			1		1	2				

	LOWGRAK				UPPGRAK			
	13	14	15	16	4	5	6	7
Atlantic Ocean	1	2	4		1	5		1
Japan and Kyushu Palau Ridge	5	3*			4	4*		
Australia and New Caledonia			1	1			2	

apply to our Atlantic material as well as to his paratype (BSKU 29532). Differences between our description and Okamura's appear to be attributable to methodology. For example, Okamura reports 4-5 first dorsal fin rays compared to our report of 6. Our count includes all elements, which here includes a small first element not normally seen without radiographs or dissection. We found no meristic characters (Table 6) to differentiate *L. robustum* from *L. filodorsale, L. modestum*, and specimens from off eastern Australia and New Caledonia. We tentatively treat *L. filodorsale* and *L. modestum* as junior synonyms of *L. robustum*, but note the small sample sizes and the potential that slight differences might exist.

Laemonema robustum is morphologically similar to *L. macronema* n. sp., from the western Indian Ocean, and *L. yuvto*, from the eastern Southern Ocean, in the robustness of the body, the low fins ray and vertebral counts, and the high pectoral fin ray counts. *Laemonema robustum* differs from *L. yuvto* in having fewer second dorsal fin rays (50-57 vs 62). Differences with *L. macronema* are discussed below.

Color in alcohol. —Body light brown; visceral area gray; first dorsal fin and anterior portion of second dorsal fin dark brown.

Distribution. —This species is widely distributed around oceanic islands and trenches in the Atlantic and Pacific over a depth range of 336-1200 m. In the Atlantic, it is found from the eastern North Atlantic near Madeira, the type locality, to Saint Helena Island (15° 58'S, 5° 43'W) in the tropical South Atlantic. Most specimens from the Atlantic were collected in the fish market at Funchal, Madeira, with no depth of capture data available. In the Pacific, *L. robustum* is found from the Kyushu-Palau Ridge to New Caledonia and Australia at depths from 540 to 1200 m (Fig. 25). This wide distribution is similar to that of the morid, *Antimora rostrata*, which is distributed in all oceans except the North Pacific (Small, 1981).

Material examined. —Holotype - BM(NH)1862.6.9 (1, 311), tail regenerated, Madeira Island. paratype-BSKU 29532. others - BM(NH)1969.3.1, CAS 123939, MMF 52, MMF 3127, MMF 3128, MMF 3461, MMF 3512, MNHN 1986-295, MSU P 16049, QM I.21006.

Laemonema yarrelli (Lowe, 1838)
Figure 21d

Phycis yarrelli Lowe,1838: 190 (we follow Eschmeyer (1990) in using 1838 rather than 1841 as used by others.
Laemonema yarrelli: Günther 1862: 356. Goode and Bean, 1896, 2:362. Holt and Byrne, 1908a:87. Taki, 1953: 208. Rass, 1954: 8. Matsubara, 1938: 62. Parin, 1984:57. Cohen,1986:717. Edwards and Glass, 1987:630. Biscoito and Maul, 1989:2-6. Cohen, 1990: 552. Cohen et al., 1990: 361.
Laemonema curtipes Biscoito and Maul, 1989:1-8.
Laemonema curtipes: Cohen et al., 1990:361.

Diagnosis. —Body low and slender, covered with small, deciduous scales; second ray of first dorsal fin long, 17.1-27% SL; vertical fins with a marginal black stripe.

Description. —Head short, 20.2-23.6% SL. Mouth large, maxillary 9.5-10.9% SL, with at least six rows of teeth decreasing in size from outer row to inside row. Dentition of dentary similar to maxillary but with fewer rows of teeth. Teeth on small oval patch on vomer. Barbel present 3.2-5.4% SL. Snout 5.6-6.9% SL, without scales. Eyes large, orbit diameter 6.3-7.6% SL, greater than interorbital width, 3.7-5.0% SL. Postorbital length 6.9-21.2% SL.

Predorsal length 21.5-27.9% SL, greater than head length. Maximum body depth 16.8-21.2% SL, similar to depth at anus, 16.6-20.9% SL. Prepectoral length 22.3-26.2% SL, about same as predorsal fin length. Prepelvic length 14.8-22.6% SL. Preanus length 32.2-40.3% SL, slightly less than preanal fin length 35.3-43.5% SL. Body tapering to caudal peduncle, the depth of which is 1.8-2.6% SL.

First dorsal fin with six rays, its base 3.6-5.7% SL, second ray longest, 17.1-27% SL, very strong; first ray beneath the skin. Second dorsal fin with 58-62 rays (X = 59.6, mode = 59, cv = 1.8), its base 64.6-71% SL, rays gradually decrease towards end of fin. Anal fin with 57-62 rays, its base 54.7-61.4% SL, rays decrease moderately to middle of fin, then increases again. Pectoral fin with 21-25 rays, its base 3.5-4.8% SL, its length 15.6-19.5% SL. Pelvic fin rays with two long rays, its length 10.8-26.2% SL; rays do or do not reach anus. Caudal fin asymmetrical, upper procurrent rays 6-7, principal rays 6, lower procurrent rays 10-12. Total vertebrae 52-54 (eastern Atlantic) and 55-56 (Bermuda), precaudal vertebrae 15-16 (eastern Atlantic) and 16-17 (Bermuda), caudal vertebrae 36-38 (eastern Atlantic) and 39 (Bermuda). Gill rakers 6-8+ 14-18, total=20-25. Scales on a straight line 100-111, scales above lateral line 8-9, scales below lateral line 18-23.

Comparisons. —*Laemonema yarrelli* is most similar to *L. barbatulum* in first dorsal fin height and coloration of the dorsal and anal fins. Key differences were discussed above. The Bermuda specimens accentuate vertebral differences between the two species, showing higher precaudal counts (16-17) than either eastern Atlantic *L. yarrelli* (15-16) or western Atlantic *L. barbatulum* (13-15).

Color in alcohol. —Recently collected specimens from Russian vessels have a light-brown body. Color of first dorsal fin most conspicuous, with a black membrane. Second dorsal and anal fins have black tips.

Distribution. —*Laemonema yarrelli* is restricted to seamounts and islands in the subtropical Atlantic; in the eastern Atlantic at depths of 220-550 m and off Bermuda in 235-1640 m. Lowe's (1838) type locality is Madeira and other specimens were captured from The Meteor Seamount (29° 57'N, 28° 15'W), the Seine Seamount (33° 45'N, 14° 20'W) at 220 m, Bermuda, and off Angola (Fig. 24). Cohen (1990) describes it as benthopelagic on the outer shelf and upper slope.

Comments. —This species has been considered rare. The original description by Lowe (1838) was poor but improved by Günther (1862). Günther stated that the pectoral fin is rather longer than the pelvic fin, its length being equal to the distance of the anterior margin of the orbit from the extremity of the operculum. The specimens we examined had pectoral fin lengths of 15.6-19.5% SL and pelvic fin lengths of 16.0-26.2% SL. Thus, the pelvic fin is longer than pectoral fin. Pelvic fin length and barbel length were used by Biscoito and Maul (1989) to describe *L. curtipes*. Barbel length has a positive allometric relationship with size (unpublished, the relationship for all *Laemonema* has an r = 0.77), and all meristic characters of *L. curtipes* are within the range of *L. yarrelli*.

Material examined. —MMF 13874, MMF 22386, MMF 22543, MMF 23858 (holotype of *Laemonema curtipes*), MSU P16047, PPSIO uncat. (2, 154-155), USNM 304472, BAMZ 1995-124-007, BAMZ 1994-121-013, BAMZ 1994-121-012, BAMZ 1994-121-015.

Figure 26. *Laemonema macronema*, n. sp., holotype, RUSI 8549, 254 mm SL male, Reunion Island, June 1966.

Laemonema macronema new species
Figure 26

Diagnosis. —Pelvic fin rays long, 49.2-63.6% SL, reaching posteriorly to mid-length of anal fin; body depth slender, 23.9-24.2% SL, covered by small, deciduous scales; pectoral fin with 27 rays.

Description. —Head 24.4-27.4% SL, mouth subterminal. Snout short, 7.3-8.3% SL. Maxillary with an external row of conspicuous canine-like teeth, and two or three rows of small villiform teeth. Dentary with two rows of canine-like teeth, external ones larger than internal teeth. Teeth on vomer canine-like, in a round patch. Barbel on chin, 4.5-5.9% SL, smaller than or almost equal to orbit diameter. Orbit diameter large, 5.3-5.6% SL, at least five times into head length. Interorbital width short, 4.6-4.9% SL, 5.5 times in head length, almost equal to, or a bit shorter than, orbit diameter. Maxillary 12.8-13.5% SL, reaching vertical through posterior of pupil. Opercle bone ending in a thin spine on its upper portion. Postorbital length 12.5-14.1% SL.

Greatest depth of body around area of anus, 23.9-24.2% SL. Depth at first anal ray 23.2-24.0% SL. Anus and anal fin separated by a short distance, almost equal to height of caudal peduncle. Preanus length 39.8% SL. Preanal fin length 43.1% SL. Predorsal length 30.2-31.5% SL. Depth at anus 23.1-23.6% SL. Caudal peduncle depth 3.0-3.1% SL.

First dorsal fin with 6 rays, base short, 4.2-4.4% SL; first ray included in skin; second ray longest 16.9-25.2% SL; remaining rays gradually decrease in length. Second dorsal fin with 57-58 rays, base large, 59.3-60.5% SL, ray lengths gradually decrease from beginning to middle of fin, then increase to end of fin. Anal fin rays 54-55, shorter than

second dorsal fin; base length 49.6-54.2% SL. Pectoral fin with 27 rays, prepectoral length 27.6-28.0% SL, its base 4.0-4.2% SL. Pelvic fin with two elongated rays, their length 49.2-63.6% SL, reaching middle of anal fin in well-preserved specimens. Caudal fin asymmetrical, 11-13 lower procurrent caudal fin rays, upper procurrent caudal fin rays 8, principal caudal rays 6. Total vertebrae 49-51, precaudal vertebrae 14, caudal vertebrae 35-37. Gill rakers 4-5+12-13, total = 16-17. Lateral line not well defined, scale count on a straight line, about 126-125. Scales above lateral line 10-11, scales below lateral line 23-24.

Comparisons. —This species is distinctive among species of *Laemonema* because of its long pelvic fins. With *L. robustum* it shares similar morphometric and meristic characters, swimbladder shape, and a groove in struts 2 and 3 of the third pharyngobranchial. *Laemonema macronema* differs from *L. robustum* in having fewer upper procurrent caudal fin rays (8 vs 10-12), fewer scales above lateral line (10-11 vs 14-19), and fewer scales below lateral line (23-24 vs 39-47). *Laemonema macronema* differs from *L. yarrelli* in having more pectoral fin rays (27 vs 21-25) and fewer lower gill rakers (12-13 vs 14-18). *Laemonema macronema* differs from *L. melanurum* in having more total vertebrae (53-57 vs 49-51), fewer scales on a straight line (125-126 vs 145-166), fewer scales above the lateral line (10-11 vs 18), fewer scales below the lateral line (23-24 vs 35-36), and in lacking the color pattern of the second dorsal, anal and caudal fin. *Laemonema macronema* differs from *L. rhodochir* in having fewer second dorsal fin rays (57-58 vs 61-66), fewer anal fin rays (54-55 vs 58-63), and more pectoral fin rays (27 vs 22-24). *Laemonema macronema* differs from *L. yuvto* in the lower counts of the second dorsal fin (57-58 vs 62), and pectoral fin (27 vs 31).

Color in alcohol. —Body light brown, vertical fins with blackish margin and whitish tips on rays of second dorsal and anal fins, and most of caudal fin. Pectoral fin dark brown, with light brown edges. Pelvic fins light brown to whitish. Mouth and gill chamber light brown.

Distribution. —*Laemonema macronema* has been found only off Reunion and Mauritius Island (Mascarene Islands) in the Indian Ocean at depths of 300-400 m (Fig. 25).

Etymology. —In recognition of its long (macro) leggings or fin rays (cnemis), the name should be treated as a noun in apposition.

Material examined. —Holotype: RUSI 8549, a 254 male, Reunion Island, June 1966, collected by Gueze.

Paratypes. —RUSI 1423, (1, 230+, tail broken,cleared and stained), MNHN 1966-848. (1, 236).

Laemonema goodebeanorum new species
Figure 27

Diagnosis. —Second dorsal fin with 66-73 rays, modally 70; height of first dorsal fin 10.1-17.1% SL, with an average of 13.8% SL; narrow interorbital 3.4-4.7% SL; orbit diameter 6.4-8.3% SL.

Description. —Body fusiform, covered with moderate-sized scales. Head short, 20.0-24.0% SL; maxillary 9.2-11.7% SL, almost reaching middle of pupil, with one outer row of strong caniniform teeth followed by five or six rows of small inner teeth. Vomer with a rounded patch of teeth. Dentary dentition as in maxillary, but with two or three rows of

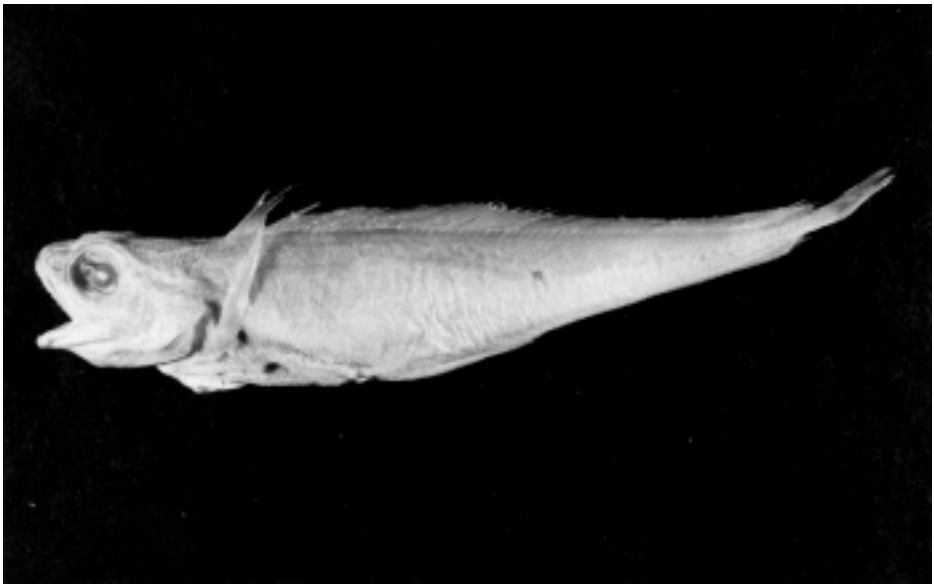

Figure 27. *Laemonema goodebeanorum*, n. sp., paratype, UF 45373, 244 mm SL.

small inner teeth. Orbit diameter greater than the interorbital width, 3.4-4.7% SL. Postorbital length 8.8-10.7% SL, the opercle ending in a flat and wide spine.

Predorsal length 21.4-27.6% SL, D1 inserted at about same level as pectoral fin. Prepectoral length 20.5-26.0% SL. Preanal length 37.8-45.7% SL, anus close to anal fin, preanus length 35.5-44.0% SL. Maximum depth of body around area of anus, 14.0-20.6% SL. Body depth at first anal fin ray 12.2-19.3% SL. Caudal peduncle depth 1.7 - 2.5% SL.

First dorsal fin with six rays (one specimen with five), the first ray beneath skin; second ray largest. Dorsal fin base 3.0-7.9% SL. Second dorsal fin with 66-73 rays (mean = 69.6, mode = 70, cv = 2.3), its base 63.4-71.0% SL. Anal fin with 65-71 rays (mean = 68, mode = 67, cv = 2.5), its base 51.8-59.9% SL. Pectoral fin with 19-22 rays (mean = 20.3, mode = 20, cv = 3.5), its base 2.5-3.7% SL, its length 12.0-17.3% SL; inserted before insertion of first dorsal fin; prepectoral length 20.5-26.0% SL. Pelvic fin with two rays, which reach fourth or fifth anal ray; fins inserted well before pectoral fin. Prepelvic length 14.7-24.7% SL. Caudal fin asymmetrical, upper procurrent rays 8-11 (mean = 8.6, mode = 9, cv = 7.9), six principal caudal rays, lower procurrent rays 12-16 (mean = 14.0, mode = 14, cv = 6.9). Total vertebrae 56-59 (mean = 57.6, mode = 57, cv = 1.5), precaudal vertebrae 15-17 (mean = 16.2, mode = 16, cv = 2.9), caudal vertebrae 39-43 (mean = 41.3, mode = 41, cv = 2.2). Gill rakers 7-9 (mean = 7.8, mode = 9, cv = 7.0)+17-20 (mean = 18.3, mode = 18, cv = 4.6), total = 24-29. Scales on a straight line 125-143; scales above lateral line 10-13 (mean = 11.6, mode = 12, cv = 10.2).

Comparisons. —This species is very similar to the allopatric *L. laureysi* Poll from the subtropical and tropical eastern Atlantic. Although there is overlap in most characters (Table 7), they occupy different multivariate space based on both morphometric and meristic characters. Principal components analysis of HL, PDL, PAL, PANUS, UJL, SNT, ORB, INT, D2L, AL, and CAUDDEPTH separated the two groups, with few specimens

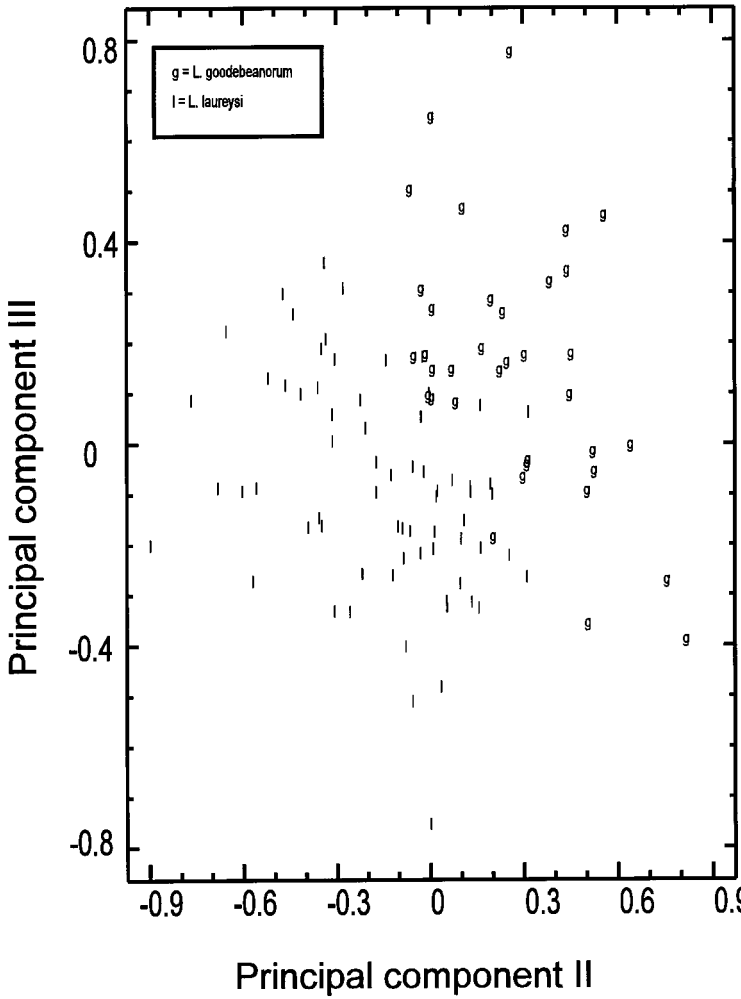

Figure 28. Second and third principal component axes for selected morphometric characters for *Laemonema goodebeanorum* and *Laemonema laureysi.*

of *L. laureysi* overlapping *L. goodebeanorum* (Fig. 28). Discriminant analysis of these morphometric characters correctly distinguished all specimens. Principal component analysis of meristic characters DI, D2, A, P1, PCV, CV, UGR, LGR, UPPCR, and LPCR also separated the two species, but with more overlap (Fig. 29). Discriminant analysis using the meristic characters correctly classified 100% of *L. goodebeanorum* and 94.24% of *L. laureysi*.

Laemonema goodebeanorum differs from other similar species in having more second dorsal fin rays (66-73) compared to *L. gracillipes* (56-63), *L. yarrelli* (58-62), and *L. longipes* (49-53); more anal fin rays (65-71) compared to *L. gracillipes* (55-61), *L. yarrelli* (57-62), and *L. longipes* (48-52); more total vertebrae (56-59) compared *L. yarrelli* (52-56); fewer lateral line scales (125-143) compared to *L. gracillipes* (155-172), *L. yarrelli* (100-111); and a rounded vomer compared to the v-shaped vomer of *L. longipes.*

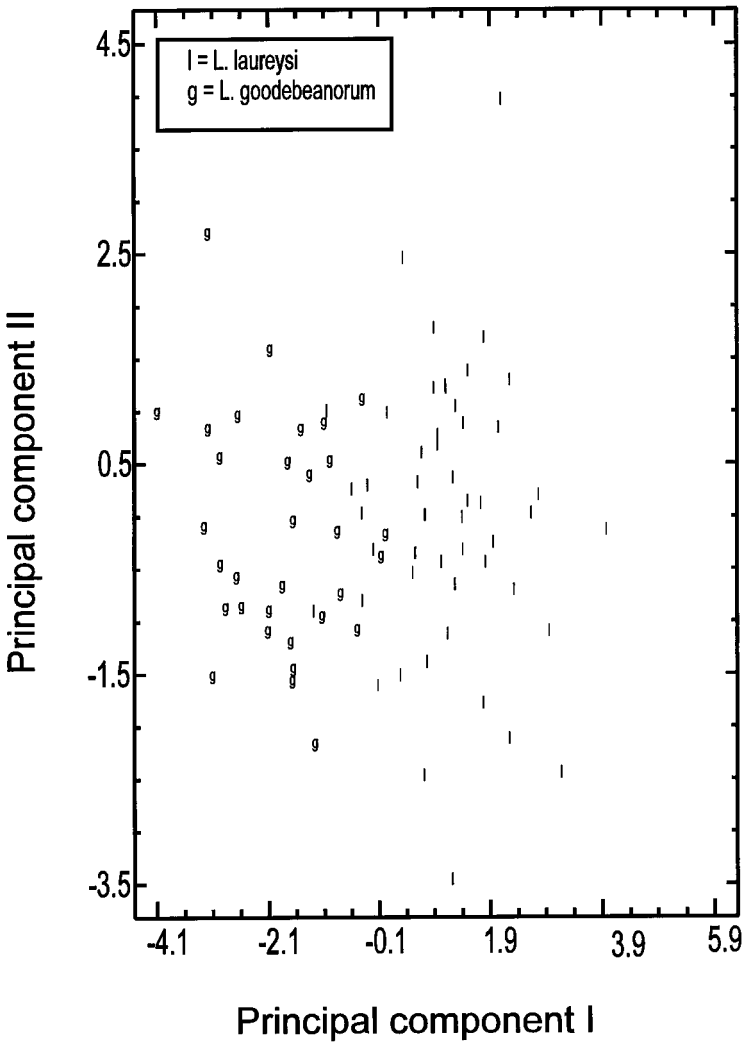

Figure 29. First and second principal component axes for meristic characters for *Laemonema goodebeanorum* and *Laemonema laureysi.*

Color in alcohol. —Body light gray to pinkish-white in a few specimens; all fins dusty brown to whitish but first dorsal with black tips on rays.

Juveniles. —A single juvenile, MCZ 85898, 44.2 mm SL, was found. It is similar in shape to comparably sized *L. barbatulum* (Fig. 22a), but differs conspicuously in having rectangular brown spots on the second dorsal and anal fins. There are possibly five spots on the second dorsal and seven on the anal fin. Each spot covers about five rays. As in the other two juveniles of *Laemonema* at this size (Fig. 22), there is a small area at the end of caudal skeleton without pigmentation. Color of body light brown, head paler; area of viscera brown; highly pigmented area between insertion of pelvic fins; pelvic fins with melanophores over entire length.

Body slender, head 24.0% SL, orbit diameter 7.2% SL, interorbital width 5.0% SL. Predorsal length 27.6% SL, prepelvic length 17.0%, preanus length 39.1% SL, preanal fin length 41.9% SL, D2 length 64.5%, A length 53.8% SL, caudal peduncle depth 2.3% SL. Six first dorsal fin rays, 71 second dorsal fin rays, 65 anal fin rays, 21 pectoral fin rays, seven pelvic fin rays. Caudal fin asymmetrical, upper procurrent caudal rays 9, principal caudal rays 6, lower procurrent caudal rays 14. Total vertebrae 57, precaudal vertebrae 16, caudal vertebrae 41. Gill rakers 8+17.

Distribution. —*Laemonema goodebeanorum* is widely distributed on the continental slope in the western Atlantic, from off Canada 42°38'N, 64°19'W to off southern Brazil, 25° 24'S, 44° 54'W, including the Gulf of Mexico, off French Guiana, and off Suriname; depth range 180-792 m (Fig. 25).

Etymology. —This form was apparently recognized by G. B. Goode and T. H. Bean based in part on the type series used herein. Here named in recognition of their monographic work on deep sea fishes. The name should be treated as an adjective.

Material examined. —Holotype: USNM 045967 (169, female), 28° 34'N, 86° 48'W, 11 II 1885. Paratypes: USNM 158228 (1, 236), 29° 11'N, 86° 52'W, 24 II 1951. USNM 213496 (1, 149), 36° 58'N, 74° 38'W, 613 -710 m, 17 IV 1974. USNM 158090 (1, 104.7), 29° 10'N, 88° 07'W, 24 VI 1956. USNM 304409 (1, 92.3), 09° 47'N, 79° 25'W, 230 fm, 19 X 1965. UF 44376 (2, 137-221), 29° 09'N, 88° 03'W, 190-191 fm, 21 I 1986. UF 45373 (1, 244), 14° 10'N, 81° 50'W, 300-330 fm, 21 V 1962. MCZ 57923 (1, 186), 11° 36'N, 62° 46'W, 290 fms, 19 IV 1960., MCZ 45983 (1, 198), 11° 53'N, 69° 25'W, 350 fms, 3 X 1963., LACM 43471-1 (2, 139-140), ARC 8600883 (3, 207-262-269), 42° 38'N, 64° 19'W, 360 m, 30 VIII 1986.

Material examined but excluded from the type series. —ARC 8600821 (1, 190), ISH 1066/66 (2, 165-182), ISH 1887/68 (2, 120-228), MCZ 85898 (1, 44.2), UF 39976 (2, 112-125), UF 39993 (2, 158-202), UF 40041 (2, 180-219), UF 40126 (1, 203), UF 40284 (2, 209-216), UF 44376 (4, 87-246, one specimen cleared and stained). UF 45373 (2, 244-255), UF 39956 (1, 217), USNM 45965 (1, 225), USNM 45968 (1, 91.7), USNM 44231 (2, 220-227), USNM 304410 (1, 77.2).

Materials identified for distribution only are deposted in MCZ (2 spec.) and USNM (247 spec.).

Laemonema laureysi Poll, 1953

Figure 30

Laemonema laureysi Poll,1953: 197-200.

Laemonema laureysi: Parin,1984: 57. Cohen, 1986:327. Lloris, 1986: 252-254. Cohen,1990:552, Cohen et al., 1990: 361.

Diagnosis. —Second dorsal fin with 63-72 rays; height of first dorsal fin 11.9-29.2% SL; body slender, depth 11.9-22.4% SL, covered with deciduous scales.

Description. —Head short 21.9-25.1% SL. Mouth broad, maxillary 10.2-12.5% SL, reaching middle of pupil, with two outer rows of strong canine-like teeth and four or more rows of small teeth. Vomer rounded, with teeth. Dentary with same type of teeth as in maxillary. Barbel 2.7-4.7% SL, always present. Snout short, 5.4-7.4% SL. Orbit diameter 6.3-8.8% SL, almost double interorbital width, 3.2-4.6% SL. Postorbital length 9.5-11.8% SL.

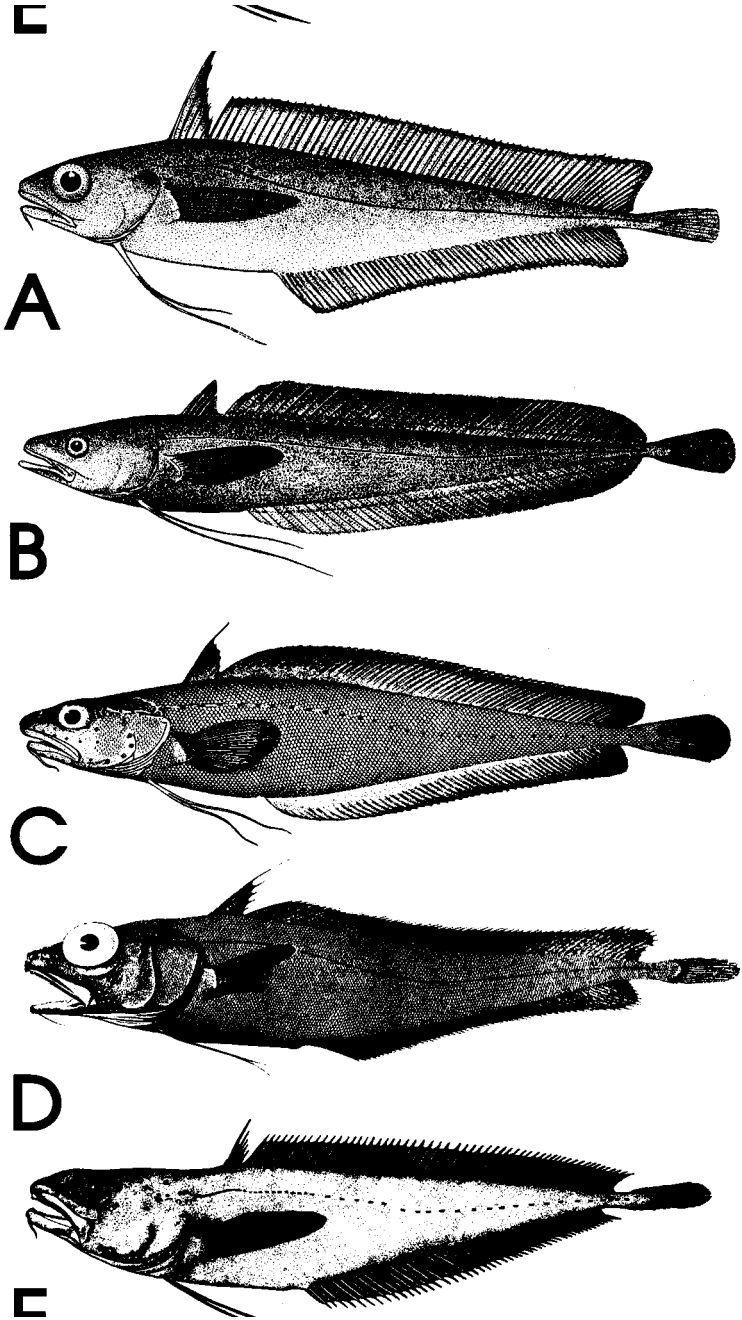

Figure 30. A. *Laemonema laureysi*, from Cohen et al., 1990 fig. 783; B. *Laemonema longipes* from Cohen et al., 1990 fig. 785; B.; C. *Laemonema rhodochir*, holotype, USNM 51623, 116 mm SL, from Gilbert, 1905, fig. 255.; D. *Laemonema gracillipes*, from Garman, 1899, pl. 42; and E. *Laemonema yuvto*, from Parin and Sazonov, 1990

Predorsal length 22.7-27.5% SL. Anus and anal fin not separated; preanus length 34.4-43.9% SL; preanal length 36.9-46.2% SL. Maximum depth of body 11.9-22.4% SL. Depth at first anal ray 13.1-23.5% SL. Prepectoral length 15.9-26.5% SL. Prepelvic length 14.9-25.5% SL. Caudal peduncle narrow, its depth 1.9-2.8% SL.

First dorsal fin with 5-7 rays, its base 2.3-5.0% SL; first ray embedded; second ray is longest, 11.9-29.2% SL. Second dorsal fin with 63-72 rays, its base 63.3-72.0% SL. Anal fin with 60-69 rays, its base 50.0-58.1% SL. Pectoral fin with 19-23 rays, its base 2.7-3.9% SL, its length 12.7-18.6% SL. Pelvic fin with two long rays, which reach and extend beyond anus; length 23.1-42.5% SL. Caudal fin asymmetrical, upper procurrent rays 7-10, principal caudal rays 6, lower procurrent rays 10-15. Total vertebrae 53-58, precaudal vertebrae 14-17, caudal vertebrae 38-43. Gill rakers 5-8+16-21, total = 22-29. Scales on a straight line 120-140, scales above lateral line 10-13. Scales below lateral line 22-24.

Comparisons. —*Laemonema laureysi* is one of the most abundant *Laemonema* in museums. It is most similar to *L. goodebeanorum* from which it can be distinguished by a combination of characters (see above). *Laemonema laureysi* differs from *L. longipes* in having more second dorsal fin rays (63-72 vs 49-53), more anal fin rays (54-55 vs 48-52), and a round vomer compared to a v-shaped vomer in *L. longipes*. *Laemonema laureysi* differs from *L. yarrelli* in having more second dorsal fin rays (63-72 vs 58 -62), more scales on a straight line (120-140 vs 100-111), and in lacking the coloration pattern of the vertical fins in *L. yarrelli*.

Color in alcohol. —Body mainly light gray, with area near viscera darker. Areas above head and near vertical fins dark. Vertical fins and caudal fin dark; pectoral and pelvic fin whitish.

Distribution. —This is a benthopelagic species of the upper continental slope (Cohen et al., 1990), found from the Mauritania upwelling area to Namibia in the subtropical and tropical eastern Atlantic (Fig. 25), at depths of 220-618 m.

Material examined. —IRSB 175 (paratypes). LACM uncat. (R/V Dr. Nansen off Angola), MMF 3316, MNHN 1987-1027, MNHN 1967-797, MCZ 56974, MCZ 86749, MSU uncat. (10° 54'S, 13° 22'E, 520 m, 24 II 1976), MSU uncat. (ca. 18 -19° S, 11° 30' E, ca. 300 m. off Namibia, 27 I 1988), MSU 11423, MSU uncat. (03° 17'S, 09° 33'E, 500 m, 19 IV 1976), PPSIO uncat. (18° 50'N 16° 50'W, 450-470 m), PPSIO uncat. (7° 43'N, 16° 41'W), PPSIO uncat (4° 50'N, 5° 24'W, 300 m 27 I 1967), PPSIO uncat. (4° 50'N, 5° 24'W, 300 m 27 I 1967), UF 47559, UF 47560, USNM 300892, USNM 301096, USNM 301096.

Material identified for distributional information are deposited in MNHN (7 spec.) and USNM (57 spec.)

Laemonema longipes (Shmidt, 1938)

Figure 30

Laemonema longipes Shmidt, 1938: 655.
Laemonema longipes: Okamura,1984:91, Cohen et al., 1990.
Podonema longipes: Rass, 1954: 2.
Podonematichthys longipes: Whitley, 1965: 25.
Laemonema morosum Matsubara, 1938: 61-62.

Diagnosis. —Body long, slender, covered by small, deciduous scales; second dorsal fin with 49-53 rays; vomer with teeth in a V-shape; no barbel on chin.

Description. —Head 20.2-24.6% SL; mouth subterminal. Snout large, 6.3-7.5% SL. Maxillary with an external row of conspicuous canine-like teeth, with two or three inner rows of small villiform teeth. Dentary with two rows of canine-like teeth, external ones largest, internal teeth smaller. Teeth on vomer canine-like, in a v-shaped patch. No barbel on chin. Orbit diameter 3.5-5.6% SL, almost 5.0 in head length. Interorbital width broad, 3 in head length, and almost 1.5 in orbit diameter, 5.9-7.3% SL. Maxillary 9.0-11.8% SL, ending at about same height as the posterior end of pupil. Opercle bone ending in a spine in its upper portion. Postorbital length 10.8-13.0% SL.

Greatest depth of body around area of anus, 12.6-18.5% SL. Body depth at first anal ray 11.8-15.5% SL. Anus and anal fin separated by a short distance, shorter than height of caudal peduncle. Preanus length 32.5-36.4% SL. Preanal fin length 33.9-38.0% SL. Predorsal length 22.3-27.0% SL. Depth at anus 11.8-15.4% SL. Caudal peduncle depth 1.4-2.6% SL.

First dorsal fin with 6 rays, short base 4.7-7.1% SL; first ray not embedded, second ray longest, 8.4-12.6% SL, remaining rays gradually decrease in length. Second dorsal fin with 49-53 rays, base long 61.6-69.3% SL, ray lengths gradually decrease from beginning to end. Anal fin with 48-52 rays, base lightly shorter than second dorsal fin 58.6-62.6% SL. Pectoral fin ray with 16-18 rays, its base 2.5-3.2% SL; prepectoral length 21.0-25.6% SL. Pelvic fin with two elongated rays, its length 26.4-42.3% SL, reaching anus. Caudal fin asymmetrical, 9-11 lower procurrent rays, upper procurrent rays 7-8, principal rays 5-6. Total vertebrae 49-52, precaudal vertebrae 14-16, caudal vertebrae 34-37. Gill rakers 7-8+18-20, total = 26-28. Lateral line not well defined, count on straight line about 110-144 scales. Scales above lateral line 10-11, below lateral line 20-25.

Comparisons. —*Laemonema longipes* differs from most other *Laemonema* in the absence of a barbel, presence of a v-shaped vomer, and in the shape of the swimbladder. Only *L. verecundum* shares a crescent or v-shape vomer and approximately the same shape of swimbladder, but *L. verecundum* has more (8-9 vs 6) first dorsal fin rays and an elongate caudal peduncle.

Color in alcohol. —Body grey; second dorsal fin, caudal and anal fins with blackish tips.

Distribution. —*Laemonema longipes* is distributed in the western North Pacific, from off Owase, Japan to the eastern Bering Sea (Yabe et al., 1981; Cohen et al., 1990) (Fig. 24). Cohen et al. (1990), considered this fish as benthopelagic on the continental slope from 455 to 1400 m depth. It is one of the few morids considered to be a commercial resource (Cohen et al., 1990). It is locally abundant in the Sea of Okhotsk (Shmidt, 1950) and off Japan where commercial concentrations occur at 200-800 m (Pautov, 1980). It is the best studied *Laemonema* with several recent Japanese and Russian articles on its biology and fishery.

Material examined. —CAS 47657, HUMZ 81033, HUMZ 81034, HUMZ 81035, PPSIO uncat. (Sea of Okhotsk, st 155), USNM 161488, USNM 149844, USNM 150362, USNM 220877.

Laemonema rhodochir Gilbert, 1905

Figure 30

Laemonema rhodochir Gilbert, 1905: 657-658.
Laemonema rhodochir: Taki,1953:8. Rass,1954:5. Parin, 1984: 56-59. Cohen et al., 1990: 361. Parin and Sazonov, 1990:8.
Laemonema palauense Okamura, 1982:136-139.
Laemonema palauense: Okamura,1984:92. Parin and Sazonov, 1990:8.

Diagnosis. —Body low and slender, covered by small deciduous scales; conspicuous pores below eye; lower gill arch with 11-14 gill rakers; pectoral fin with 22-24 rays

Description. —Head length 22.2-24.9% SL. Maxillary 9.7-11.9% SL, reaching end of pupil, with two rows of strong canine-like teeth followed by three rows of smaller teeth. A rounded patch of canine-like teeth on vomer. Dentary with four or more rows of similar-sized caniniform teeth. Snout 6.5-7.6% SL, without scales. Barbel 3.3-5.6% SL, always present, longer than interorbital width. Orbit diameter 5.1-7.0% SL, longer than interorbital width, 3.4-4.9% SL. Superior area of orbit with two pores. Postorbital length 10.1-24.9% SL.

Predorsal fin length 25.1-29.4% SL. Anus and anal fin not separated. Preanal fin length 36.7-43.5% SL. Preanus length 34.1-39.7% SL. Prepelvic fin 17.8-23.6% SL. Prepectoral length 23.3-27.0% SL. Maximum depth of body below first dorsal fin 15.7-21.5% SL. Body depth at first anal ray 15.2-19.4% SL; body decreases posteriorly to caudal peduncle, 1.8 -3.1% SL, which is less than length of barbel.

First dorsal fin with six rays, its base 3.1-4.7% SL, its second ray longest, 8.3-12.6% SL; first fin ray embedded in skin. Second dorsal fin with 61-66 rays, its base 61.3-67.8% SL, length of rays decrease posteriorly. Anal fin with 58-63 rays, its length 52.5-58.5% SL, rays shorter around middle of anal fin. Pectoral fin with 22-24 rays, its base 3.3-4.5% SL, its length 16-21% SL. Pelvic fin with two long rays; in one individual only, three small rays observed beneath skin. Caudal fin asymmetrical, upper procurrent rays 7-10, six principal rays, lower procurrent rays 11-13. Total vertebrae 51-54, precaudal vertebrae 15, caudal vertebrae 36-39. Gill rakers 4-6+11-14, total = 16-19. Scales on a straight line 105-130, scales above lateral line 9-15, scales below 21.

Comparisons. —Even though the species is widely distributed, we found little evidence of differentiation. Using both single and multivariate analyses of morphometrics, we could not find any indication of geographic groupings. Parin (1984), based on general appearance and meristic counts, considered *L. palauense* a junior synonym of *L. rhodochir*. Our meristic data support Parin (Table 8).

Laemonema rhodochir is similar to *L. laureysi* and *L. goodebeanorum* as discussed above. *Laemonema rhodochir* differs from *L. robustum* in having more second dorsal fin rays (61-66 vs 50-57), more anal fin rays (58-63 vs 48-54), fewer pectoral fin rays (22-24 vs 26-30), and fewer scales below the lateral line (21 vs 39-43). *Laemonema rhodochir* differs from *L. yuvto* in having more anal fin rays (58-63 vs 53), and fewer pectoral fin rays (22-24 vs 31). *Laemonema rhodochir* differs from *L. macronema*, mainly in the length of the pelvic fin rays (19.8-35.2 vs 49-65% SL).

Color in alcohol. —Body gray, second dorsal fin dark brown to light gray to yellowish; visceral area always gray.

Distribution. —This species is distributed along the Mid-Pacific Ridge, from the Kyushu-Palau Ridge (28° 05'N, 134° 42'E), off the south coast of Oahu Island, to Sala y Gomez

Table 7.- Comparison of selected meristic characters of *Laemonema laureysi* and *L. goodebeanorum*.

	D2											A											
	63	64	65	66	67	68	69	70	71	72	73	60	61	62	63	64	65	66	67	68	69	70	71
L. laureysi	2	7	9	17	11	4	4	1		1		3	2	6	7	12	12	7	5	1	1		
L. goodebeanorum				1	2	6	6	14	3	3	3						4	3	8	6	8	6	1

	PC				CV						TV						
	14	15	16	17	38	39	40	41	42	43	53	54	55	56	57	58	59
L. laureysi	1	39	14	2	4	10	30	9	1	1	1	9	23	18	2	1	
L. goodebeanorum		1	27	9		1	2	19	7	5				3	13	12	6

Ridge in the eastern South Pacific. Okamura (1982) described it as *L. palauense* from the Kyushu Palau Ridge, and Parin (1984) listed it from the Sala y Gomez Ridge. Collected at depth from 95 to 550 m (Fig. 23).

Material examined. —Holotype - USNM 51623 (1, 104), 02° N, 02° 24'E, 53-211 fm, 27 III 1902. other - BSKU 35967 (paratype of Laemonema palauense), PPSIO uncat. (24° 47'N, 135° 20'E, 6 I 1982), PPSIO uncat. (25° 41'S, 86° 35'W, 28 IV 1987), PPSIO uncat. (25° 48'S, 86° 34'W, 28 IV 1987), PPSIO uncat. (25° 42'S, 86° 32'W, 31 X 1979), PPSIO uncat. (25° 07'S, 99° 46'W, 7 V 1987), PPSIO uncat. (25° 09'S, 90° 18'W), USNM 265089.

Laemonema gracillipes Garman, 1899

Figure 30

Laemonema gracillipes Garman, 1899: 186-188.

Laemonema gracillipes: Shmidt, 1950: 44. Rass, 1954: 8. Parin, 1984: 57. Markle and Meléndez,1988: 875. Cohen et al., 1990:361.

Diagnosis. —Head length 26.0-29.2% SL; body depth at first anal ray 14.2-19.3% SL; second dorsal fin with 56-63 rays; scales on a straight line 150-172.

Description. —Mouth broad and terminal. Maxillary 11.1-13.5% SL, reaching posterior ending of pupil. Barbel 3.8-5.0% SL. Snout short 6.3-7.8% SL. Orbit diameter 7.0-8.4% SL, greater than interorbital width 4.4-5.4% SL. Postorbital length 13.7-14.4% SL.

Predorsal length 26.4-29.8% SL, dorsal origin approximately equal with end of head. Anus and anal fin closely approximate. Preanus length 36.1-46.5% SL. Preanal fin length 38.9-50.4% SL. Maximum body depth 19.4-20.8% SL, occurring around middle of abdomen. Body depth at first ray of anal fin 14.2-19.3% SL. Prepectoral length 29.6-30.8% SL. Prepelvic length 20.6-25.4% SL. Body decreases posteriorly to caudal peduncle; caudal peduncle depth 2.2-2.6% SL.

First dorsal fin with six rays, its base 3.7-4.3% SL; second ray largest, first ray embedded. Second dorsal fin with 56-63 rays, its base 59.7-63.1% SL, rays slowly decrease in length, but lengthen again near the end of fin, then abruptly shorten over last four or five rays. Anal fin with 55-61 rays, shorter than second dorsal fin, its base 48.2-55.2% SL; a smooth reduction in lengths of fin rays towards middle of fin. Pectoral fin ray with 21-23 rays, its base 3.4-4.0% SL, its length 16.7-17.6% SL; prepectoral length 29.6-30.8% SL. Two long pelvic fin rays 23.5-29.5% SL; some specimens have 1-3 short and rudimentary rays; two longest pelvic fin rays reach at least 10th anal fin ray. Caudal fin rays asymmetrical, upper procurrent caudal rays 8-9, principal caudal rays 6, lower procurrent caudal rays 12-14. Total vertebrae 52-54, precaudal vertebrae 15-16, caudal vertebrae 37-38. Gill rakers 6-8+16-21, total = 23-29. Lateral body scales 150-172, 14-15 scales above lateral line; 30-35 scales below lateral line.

Color in alcohol. —According to the original description the body is brown, with a reddish tint; vertical and pectoral fin are blackish; pelvic fins are whitish. Specimens in alcohol were light brown, and all fins were whitish.

Distribution. —*Laemonema gracillipes* appears to be associated with islands in the tropical eastern Pacific, near the Galápagos Islands and off Panama (Fig. 30), in depths of 515-722 m.

Comments. —This species is rare and poorly represented in museums. Garman (1899) considered it to be similar in shape to *L. barbatulum* and similar in meristic features to *L.*

melanurum. Our data show that *L. barbatulum* and *L. gracillipes* are similar in fin ray counts, but differ in the number of lower gill rakers (10-13 in *L. barbatulum* vs 16-21) and scales on the lateral line (128-140 in *L. barbatulum* vs 155-172). *Laemonema gracillipes* differs from *L. melanurum* in having fewer pectoral fin rays (21-23 vs 25-27), more lower gill rakers (16-21 vs 12-15), no black triangular patch at the upper end of the second dorsal and anal fin, and no black rectangular patch in the caudal fin. *Laemonema gracillipes* differs from *L. longipes* in having more second dorsal fin rays (56-63 vs 49-53), more anal fin rays (55-61 vs 48-52), and more pectoral fin rays (21-23 vs 16 -18). *Laemonema gracillipes* differs from *L. laureysi* in having more scales on a straight line (155-172 vs 120-140), more scales above the lateral line (14-15 vs 10-13), and more scales below the lateral line (30-35 vs 22). *Laemonema gracillipes* differs from *L. yarrelli* in having more scales on a straight line (155-172 vs 100-111), more scales above the lateral line (14-15 vs 8-9), and more scales below the lateral line (30-35 vs 18-23).

Material examined. —Syntypes-MCZ 28609 (1, 169), 00° 19'N, 90° 34'W, 331 fms, 4 VIII 1981. MCZ 67155 (1, 83), 07° 32'N, 79° 6'W, 286 fms, 3 VIII 1891. other- CAS-SU 25629, USNM 135362.

Laemonema yuvto Parin and Sazonov, 1990

Description. —(from the original paper, no specimen examined) Head not globular; almost terminal mouth; maxillary extending to a vertical from posterior margin of pupil; both jaws without enlarged teeth, all teeth uniform; oral cavity unpigmented; well developed barbel; snout naked except for a band of embedded scales extending on each side from interorbital to level of anterior nostril. Interorbital space almost flat, equal to orbit diameter. D1 6, D2 62, A 53, P1 31, P2 2. Vertebrae 15+36 = 51. Modified lateral line scales 29-30, scales on a longitudinal row about 135, scales above lateral line 13. Gill rakers 13+5.

Holotype. - ZIL 49186, mature female, 191, Sala y Gomez Ridge, 25° 10'S, 90° 19'W, 1-2 May 1987, bottom shrimp trawl at 545-600 m (Fig. 30).

Comments. —According to Parin and Sazonov (1990), *L. yuvto* is related to *L. robustum* and differs mainly in the number of dorsal fin rays (62 vs 50-57). It is also similar to *L. macronema*, but differs in the length of the pelvic fin rays (26.9 vs 49.2-63.6% SL). *Laemonema yuvto* is different from all other *Laemonema* species because of the presence of modified, tubular scales on the lateral line (Sazonov, pers. comm., 1995).

Laemonema verecundum (Jordan and Cramer *in* Gilbert, 1897)

Figure 31

Lepidion verecundum Jordan and Cramer in: Gilbert, 1897: 456-457.
Microlepidium verecundum: Garman, 1899:180. Fitch and Barker, 1972; 567-568. Ambrose, 1995 (larvae).
Microlepidium grandiceps Garman, 1899.
Laemonema verecunda: Cohen et al., 1990:361.

Diagnosis. —Body slender; caudal peduncle elongate, its depth 12-15% of its length; vomer with a crescent or V-shape; first dorsal rays 8 to 9, second dorsal fin 40-42 rays, anal fin with 41 rays; barbel present, 1.2-1.7% SL.

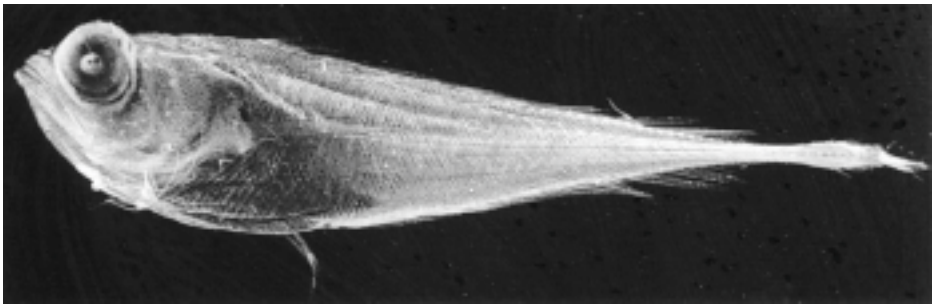

Figure 31. *Laemonema verecundum,* SIO 54-92, 80.4 mm SL.

Description. —Head 26.1-30.4% SL, mouth subterminal, slightly inclined. Snout short, 4.2-5.4% SL. Maxillary with external row of conspicuous canine-like teeth, and two inner rows of smaller canine-like teeth; a large space with no teeth at symphysis. Dentary with one row of conspicuous canine-like teeth, and one inner row of not well-defined small teeth; no symphyseal teeth gap. Teeth on vomer canine-like, in single V-shaped line. Small barbel on chin, 1.2-1.7% SL. Orbit diameter, 9.1-11.2% SL. Interorbital width short 3.6-4.7% SL. Maxillary 11.1-14.0% SL, ending at about same vertical as anterior part of pupil. Opercle ending in a spine in its upper portion. Postorbital length 15.1-15.6% SL.

Greatest depth of body around anus area, 16.5% SL. Body depth at first anal ray 14.8-17.5% SL. Predorsal length 26.1-28.7% SL. Preanal length 41.5-42.7% SL; preanus length 39.8-40.9% SL. Depth at anus 15.1-17.1% SL. Caudal peduncle depth 1.2-1.7% SL.

First dorsal fin with 8-9 rays, its base 7.9-8.4% SL; first ray very short and not embedded in skin; third ray largest, 18.7% SL. Second dorsal fin with 40-42 rays, base long, 51.0-53.6% SL. Anal fin with 41 rays, base slightly shorter than second dorsal fin base, 49.0-50.4% SL. Pectoral fin with 18-19 rays, its base 3.6-3.9% SL, prepectoral length 26.1-28.9% SL. Pelvic fin rays with two large fin rays which reach the first two anal rays, its length 28.1-30.0% SL, evidence of at least two other short rays. Caudal fin asymmetrical, 10-11 upper procurrent rays, 6 principal rays, and 13 lower procurrent rays. Total vertebrae 42-43, precaudal vertebrae 12-13, caudal vertebrae 29-31. Gill rakers 5-6+11-14, total = 17-19.

Comparisons. —This species resembles *L. longipes* and *G. nana* in having few total vertebrae, few second dorsal rays, and few anal fin rays. It differs from both species in having more (8-9) first dorsal fin rays (6 in *L. longipes* and 4-6 in *G. nana*). The high number of dorsal fin rays, the low number of caudal vertebrae, and the low counts in the second dorsal and anal fins distinguish *L. verecundum* of all other species of *Laemonema.* In addition, as in *G. nana, L. verecundum* is paedomorphic.

Color in alcohol. —Body light brown; head with branchial area yellowish; visceral area dark brown; all fins whitish.

Distribution. —Laemonema verecundum is only known from the Pacific off Mexico (Fig. 24) between about 15-28° N (Ambrose, 1995), and appears to be associated with islands and trenches. Adults are normally collected in midwater trawls and the stomachs of deep-feeding predators (Fitch and Barker, 1972).

Comments. —The paedomorphic morphology and unique meristic features of this species (Fig. 19) have generated various classifications. Jordan and Cramer (*in* Gilbert, 1897) described the species as a *Lepidion*; Garman (1899) included *L. verecundum* in *Microlepidium*; Cohen et al. (1990) included it in *Laemonema*; and Paulin (1989) indicated that *Microlepidium* and *Podonematichthys* might be synonyms. Our phylogeny (Fig. 18) supports Paulin's (1989) insight that *L. verecundum* and *L. longipes* are sister taxa.

Fitch and Barker (1972) found advanced ovarian eggs in a 67 mm specimen and a running ripe female of 83.5 mm SL. It appears that *L. verecundum* is paedomorphic. Our largest specimen is 101 mm SL (SIO 54-92) and the largest specimen known to us is reported to be 104 mm SL (SIO 93-24). It shares similar serial meristic counts with the other paedomorph in the group, *G. nana* (below). In our phylogeny these similarities are interpreted as homoplastic, but we caution that better study of the North Pacific taxa might reveal evidence of their monophyly.

Larval stages were described by Ambrose (1995). As in other *Laemonema*, the posterior body and caudal peduncle are unpigmented.

Material examined. —Holotype-USNM 47748 (1, 52), near Clarion Is. 15° 32'N, 124° 19'W, 8 IX 1889.

LACM 31118-2 (2, 60 -77.5, one specimen cleared and stained), SIO 54-92 (13, 33-101).

Guttigadus Taki, 1953

Laemonema (*Guttigadus*) Taki, 1953:201-210; type species,
Laemonema (*Guttigadus*) *nana* Taki, 1953 by monotypy).
Momonatira Paulin, 1985: 357 (type species, *Momonatira globosus* Paulin, 1985).
Paralaemonema Trunov, 1990: 81-83 (type species by original designation, *P. nudirostre* Trunov, 1990).

Diagnosis. —Head globular; interorbital length usually greater than orbit diameter; vomer absent, rounded or v-shaped; a small barbel usually present on chin; bases of dorsal and anal fin generally fleshy; highly modified scales in lateral line; pelvic fin with two large rays plus one to three smaller rays; caudal vertebrae 41-50; anus usually well separated from anal fin; known juveniles with numerous (5-7) vertical bars on sides.

Comments. —Paulin (1985) described *Momonatira* based on numerous features of *G. globosus*, one of which, the fleshy bases of the dorsal and anal fins, is supported herein as a synapomorphy of most *Guttigadus*. Trunov (1990) described *Paralaemonema* to include *P. nudirostre, P. nudicephalum,* and *P. squamirostre*. The diagnostic characters were a deeper body and a "casing" of skin on the anterior part of the bases of the dorsal and anal fins, but Trunov acknowledged the presence of the latter in *Guttigadus*. We treat *Momonatira* and *Paralaemonema* as junior synonyms of *Guttigadus.*

Guttigadus kongi (Markle and Meléndez, 1988)

Figure 32a

Laemonema kongi Markle and Meléndez, 1988: 871-876.
Laemonema kongi: Chiu et al. 1990. Cohen et al. 1990: 361.
Laemonema ? *multiradiatum* (not of Thompson,1916): Paulin, 1983:115. Pavlov and Andrianov, 1986:158.
Salilota sp.: Nakamura,1986:106-107.

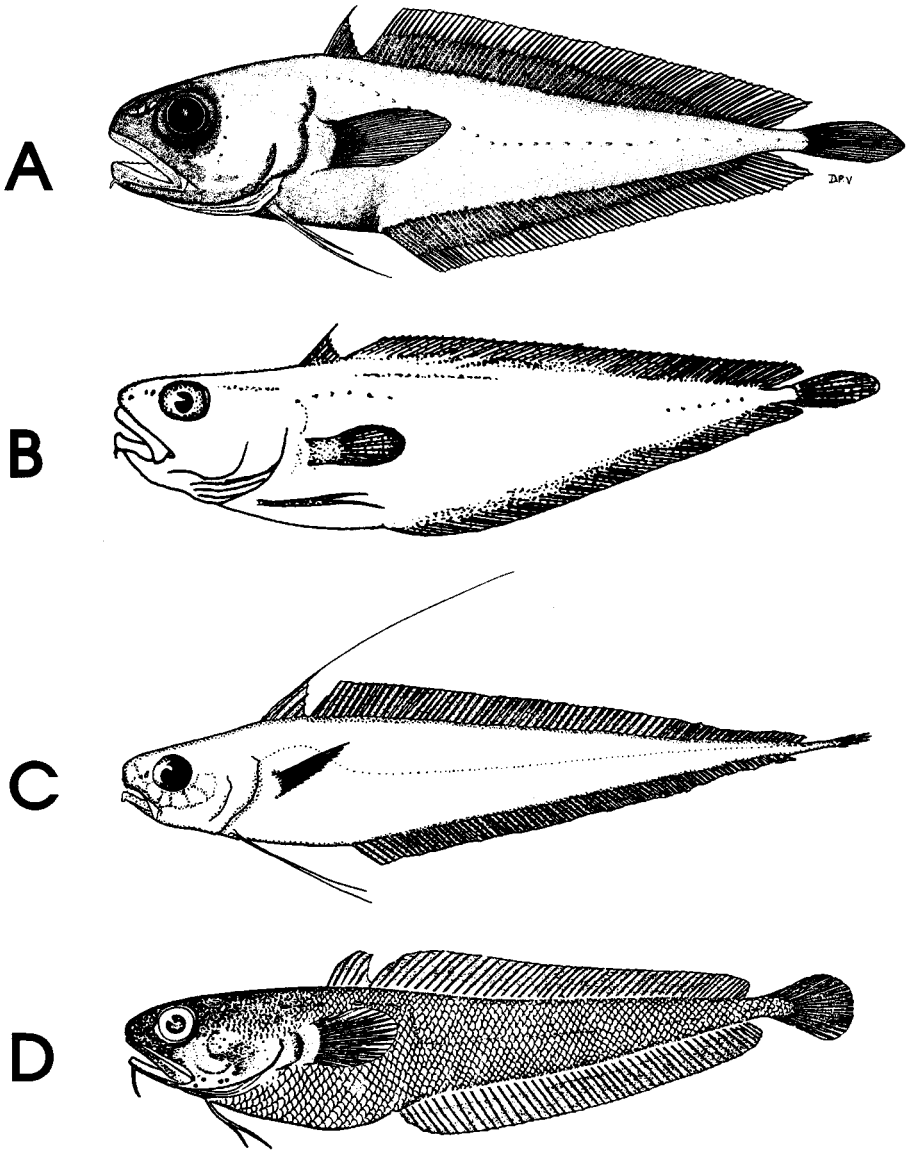

Figure 32. A. *Guttigadus kongi*, from Chiu et al., 1990, fig. 4; B. *Guttigadus latifrons*, from Cohen 1986; C. *Guttigadus globiceps*, from Paulin, 1983, fig. 21; and D. *Guttigadus nana*, from Taki, 1953.

Diagnosis. —Body short, broad, covered by small deciduous scales, ending in a very small caudal peduncle; 20-23 modified scales on lateral line; gill chamber, mouth floor and lips without pigmentation; 49-56 total vertebrae; mouth subterminal.

Description. —Head length 24.1-30.0% SL; mouth subterminal slightly inclined; maxillary with one conspicuous row of strong canine-like teeth and shorter second row of

much smaller caniniform teeth. Maxillary 12.2-15.1% SL, ending almost at end of pupil. Dentary with conspicuous row of caniniform teeth. Vomer with rounded patch of caniniform teeth. Barbel on chin short, 0.7-3.8% SL, sometimes absent. Orbit diameter short, 6.6-10.4% SL, shorter than interorbital width, 7.0-13.1% SL. Snout short, 6.6-12.9% SL, about equal to orbit diameter. Postorbital length 11.4-14.9% SL.

Predorsal fin length 26.2-32.9% SL, slightly greater than head length. Preanal fin length 35.0-48.2% SL. Preanus length 31.4-44.6% SL. Maximum depth of body around area of anus, 20.1-31.0. Depth at first ray of anal fin 17.9-29.0% SL, slightly less than maximum depth. Prepectoral fin length 26.8-33.0% SL, shorter than predorsal length. Prepelvic fin length 20.1-31.1% SL; pelvic insertion slightly anterior to pectoral fin. Body decreases in height continuously to caudal fin. Caudal peduncle depth 1.8-3.8% SL, similar to length of barbel.

First dorsal fin with 4-7 rays, second ray longest 5.5-12.1% SL; base short 3.7-7.5% SL; first ray not visible. Second dorsal fin with 62-78 rays, its base 54.6-67.6% SL; rays gradually decrease in height to end of body. Anal fin with 61-75 rays, its base 52.1-59.9% SL; a shallow depression around middle of fin. Pectoral fin with 22-27 rays, its base short 3.7-7.5% SL, its length 13.2-21.6% SL. Pelvic fin with 2 large rays and 1-4 smaller rays; longest rays reach at least 10th anal ray; length 12.7-24.7% SL. Caudal fin asymmetrical, upper procurrent rays 8-12 , principal rays 5-6, lower procurrent rays 10-14. Total vertebrae 49-56, precaudal vertebrae 10-13, caudal vertebrae 37-44. Gill rakers 6-10+13-21, total = 20-31. Lateral line with 20 to 23 modified scales, approximately 170 lateral body scales, 12 scales above, 35 scales below lateral line.

Comparisons. —Markle and Meléndez (1988) differentiated *G. kongi* from *G. latifrons* by its unpigmented mouth, lips, and gill chambers, and its lower number of caudal vertebrae. One newer specimen of *G. latifrons* (PPSIO uncat. 101.5 mm SL, Indian Ocean) has an unpigmented mouth. The new data show more overlap in caudal vertebrae (37-44 in *G. kongi* and 41-49 in *G. latifrons*), but total vertebral differences remain strong. In addition, a PCA of the morphometric characters SNT, ORB, INT, D2L, and AL, indicated two groups representing *G. kongi* and *G. latifrons*, with some overlap (Fig. 34). The important coefficients on the second axis were -0.867 (ORB) and 0.432 (INT), and on the third axis 0.559 (AL), -0.494 (INT), 0.491 (D2L), and -0.413 (SNT). Thus, *G. latifrons* tends to have longer dorsal and anal bases and *G. kongi* tends to have larger snouts, orbits and interorbital widths.

Guttigadus kongi differs from *G. nudicephalum* in having more anal fin rays (61-75 vs 56-60) and more gill rakers in the upper and lower limbs (6-10 vs 3-5 and 13-21 vs 10 -11, respectively) and *G. globosus* differs from *G. kongi* in having fewer total vertebrae (49-56 vs 56-59), more lateral body scales (170 vs 111-137), a shorter anal fin base (52.1-59.9 vs 59.9-70.2), and a pigmented rather than an unpigmented lining of the mouth.

Color in alcohol. —Body mainly pinkish (without scales); fins with dark membranes. Lips, interior of mouth, and gill chambers whitish or lightly pigmented. Juveniles with seven or eight thin, bluish vertical bands, lost at smaller sizes than in *G. latifrons* (which retains bars at sizes to 182 mm SL). Verticals bars present at 57 mm SL (NMNZ P 23396), but not in larger specimens (NMNZ P 9545, 68 mm SL, NMNZ 14852, 73 mm SL, and RUSI 27490, 86.7 mm SL).

Distribution. —*Guttigadus kongi* is found on continental slopes and some seamounts in Southern Oceans; off Chile, Argentina, Southern Australia and New Zealand, at depths of 83-1500 m (Fig. 34).

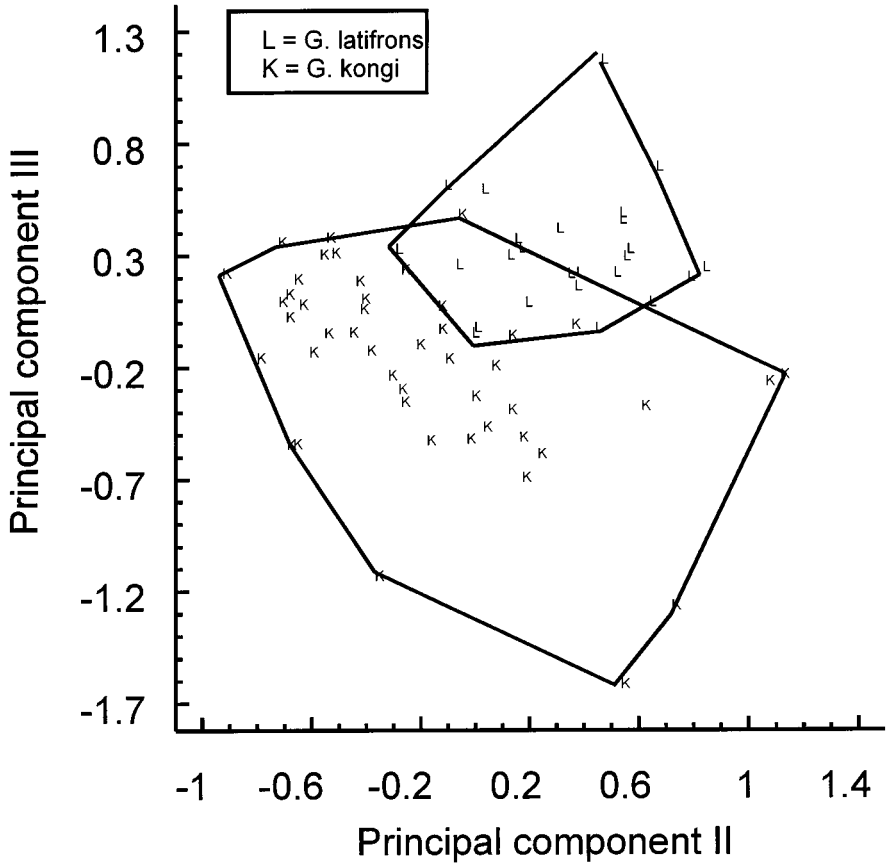

Figure 33. Scatter plot of second and third principal components for morphometric analysis of *G. kongi* and *G. latifrons*.

Comments. —One of two lots referred to *Laemonema* "sp.?" by Markle and Meléndez (1989) may be tentatively identified. The western South Pacific specimen (NMNZ P9545, 68 mm SL) appears to be a juvenile *G. kongi* based on its total vertebral count of 53, which is in the range of *G. kongi*. The two New South Wales, Australia, specimens (AMS E3210, 129 mm SL and damaged), with 59 total vertebrae remain problematic.

Material examined. —Holotype-MNHNC P6438 (1, 147), Eastern South Pacific, 34° 51'S, 72° 36'W, 690 m, 30 Aug. 1980. Paratypes-LACM 44318-1 (3, 131-135), MNHNC P6436 (1, 157), MNHNC P6437 (2, 144-145), MNHNC P6573 (5, 108-153), MNHNC P6574 (1, 112), USNM 283119 (3, 125-165). other - FAKU 348, FAKU 863, FAKU 957, ISH 277/78, ISH 1227/66, MNHNC P6589, MSU uncat. (53° 50'S, 140° 40'W, 20 V 1980), MSU uncat. (42° 38'S, 01° 34'W, 10 X 1979), MSU P13664, MSU P13657, MSU P16042, MSU P16041, MSU 13677, MSU 16503, MSU uncat, NMNZ P23396, NMNZ P14852, NMNZ P20300, NMNZ P.9545, RUSI 27490, ZIL uncat. (Chatham Ridge, eastern New Zealand, ZIL uncat. (55° 01'S, 128° 50'W, 22 XII 1972).

Material identified for distributional information are deposited in USNM (11 spec.).

Guttigadus latifrons (Holt and Byrne, 1908a)
Figure 32b

Laemonema latifrons Holt and Byrne, 1908a: 31-36.
Laemonema latifrons: Rass, 1954:8. Parin, 1984:57. Matallanas, 1985: 289-290. Cohen,1986: 717. Biscoito and Maul, 1989: 1. Markle and Meléndez, 1988: 875. Cohen et al., 1990: 361.

Diagnosis. —Body short and moderately deep; covered by small and deciduous scales; ending in small and thin caudal peduncle; 51-61 total vertebrae; mouth floor, gill chambers, and lips dark; modified scales on lateral line ca. 21-25.

Description. —Head 23.7 -27.3% SL; mouth subterminal, slightly inclined. Snout short, 6.6-8.2% SL. Maxillary with an external row of conspicuous canine-like teeth; two rows inner of small villiform teeth. Dentary with one row of canine-like teeth; two patches with large teeth near symphysis. Teeth on vomer canine-like, in a rounded patch. Barbel on chin 1.9-3.9% SL., smaller than orbit diameter. Orbit diameter, 5.7-8.2% SL. Interorbital width 7.7-10.4% SL, somewhat larger than orbit diameter. Upper jaws 10.3-13.2% SL, ending at about same vertical as posterior end of pupil. Upper border of opercle bone continuous. Postorbital length 11.6-13.5% SL.

Greatest depth of body around area of anus or between anus and insertion of pelvic fin, 16.3-27.1% SL. Depth at first anal ray 16.9-24.7% SL. Anus and anal fin separated by a distance twice or larger than height of caudal peduncle. Preanus length 29.5-38.8% SL. Preanal length 34.7-43.9% SL. Predorsal length 25.5-30.4% SL. Depth at anus 16.3-26.7% SL. Caudal peduncle depth 1.8-3.1% SL.

First dorsal fin with 5-6 rays (X = 5.6 mode = 6 cv = 9.2); base short 2.6-4.0% SL; first ray almost buried beneath skin; third ray longest, 5.3-12.2% SL., higher than caudal depth in well-preserved specimens, remaining rays slightly decrease in height. Second dorsal fin with 64-76 rays; long base, 61.6-67.1% SL, ray length gradually decreases from beginning to end of fin. Anal fin with 61-76 rays, shorter than second dorsal fin, 53.8-63.4% SL. Pectoral fin with 21-26 rays; its base 4.1-4.9% SL; prepectoral length 22.9-28.4% SL. Pelvic fin with three rays, exterior two longest; length 14.9-24.5% SL; rays reaching the anus. Caudal fin asymmetrical, 12-14 lower procurrent rays, almost equal or slightly greater than upper procurrent rays, 10-12 , principal rays 6 (one specimen with 5 rays). Total vertebrae 54-61, precaudal vertebrae 10-13, caudal vertebrae 41-49. Gill rakers 7-8+14-17, total = 21-25. Lateral line with 21-25 scales modified; scales on an straight line about 145-150. Scales above lateral line 14, below lateral line 38.

Comparisons. —*Guttigadus latifrons* is very similar to *G. kongi* and *G. globosus* (see above). The dark-mouth forms, *G. latifrons* and *G. globosus*, appear to be allopatric sister species (Figs. 42, 44), and are the deepest-living members of the genus. *Guttigadus latifrons* differs from *G. nudicephalum* in having more second dorsal fin rays (64-76 vs 59-62), more anal fin rays (61-76 vs 56-60), fewer pectoral fin rays (21-26 vs 27-28), more caudal vertebrae (41-49 vs 36-38), and more upper and lower gill rakers (7-8 vs 3-5 and 14-17 vs 10-11).

Color in alcohol. —Body mainly dark grey to light brown. Vertical fins are dark, as is the caudal fin. Lips, floor and roof of mouth, and gill chambers are dark. Juveniles have seven or eight, thin bluish vertical bands and retain them at larger sizes than *G. kongi*. Bars are present in ISH 13/82 (83 mm SL) from northwestern Atlantic, PPSIO uncataloged (82.1-114 mm SL) from Indian Ocean, and light bars in a specimen from Mediterranean Sea, off Spain, ICM uncataloged (182, mm SL).

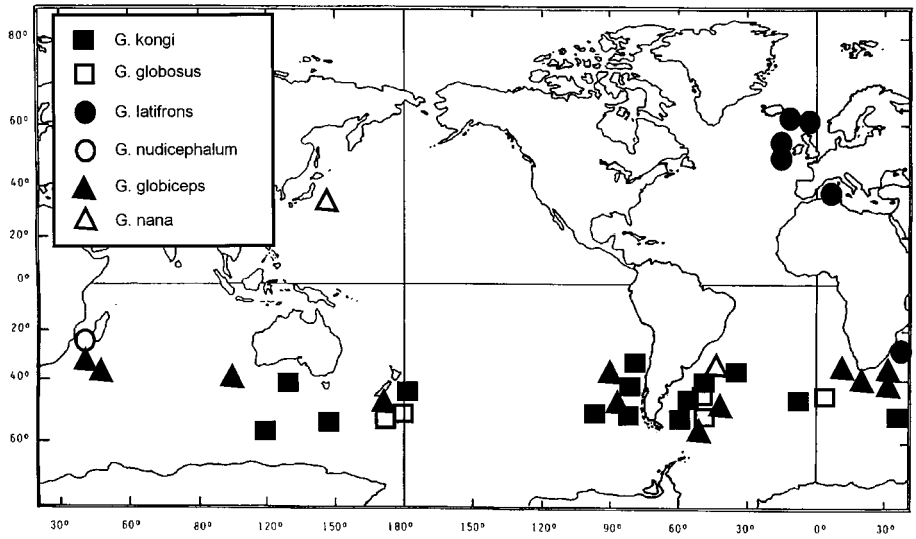

Figure 34. Species distribution chart of *Guttigadus*.

Distribution. —*Guttigadus latifrons* is reported from continental slopes in the eastern North Atlantic, Mediterranean, southwestern Atlantic (Holt and Byrne, 1908a; Matallanas, 1985; Markle and Meléndez, 1988) and western Indian Ocean (PPSIO uncat). Markle and Meléndez (1988) indicated that the southwestern Atlantic locality might have been due to a mix-up of samples. However, correspondence with ISH curator, M. Stehmann, plus a new record from the Indian Ocean suggest that the species is more widely distributed that previously thought, and that the southwestern Atlantic record is valid. The species lives in continental slope depths from 770-1875 m (Fig. 33).

Comments. —The two syntypes of this species are lost (O'Riordan, pers. comm.). We found little meristic differentiation between populations from the eastern North Atlantic and Indian Ocean, except for a suggestion of differences in caudal and total vertebrae.

Material examined. —ICM (Barcelona, Spain) uncat. (1, 182), 40° 20'-25'N, 1° 53'-56'W off Barcelona, Spain, 1715-1753 m, 3 VIII 1987. IOS 51021 (1, 108), IOS 51022 (2, 105-121 mm Sl), IOS 51305 (1, 100), IOS 9752 #1 (8, 92-140), ISH 735/74 (1, 109), ISH 738/74 (1, 4, 126-209), ISH 787/74 (1, 149), ISH 5013/79 (1, 142), ISH 30/81 (1, 139), MSU uncat. (1, 106), R/V Vityaz, sta 2673. MSU uncat. (cleared and stained) North eastern Atlantic. PPSIO uncat. (4, 82-114), 25° 09'S, 35° 36'E, 890-1000 m, 25/26 XI 1988. PPSIO uncat. (1, 88), 25° 12'S, 35° 04'E, 23 XI 1988.

Guttigadus globiceps (Gilchrist, 1906)

Figure 32c

Laemonema globiceps Gilchrist, 1906: 157-158.

Laemonema multiradiatum Thompson, 1916: 401-476.

Laemonema globiceps: Taki, 1953:8. Rass, 1954:5. Cohen, 1986. Paulin, 1983. Parin, 1984:57. Markle and Meléndez, 1988: 871. Cohen et al., 1990:361.

Laemonema multiradiatum: Rass, 1954:5.

Diagnosis. —Body low and slender, covered by small, deciduous scales ending in a small, thin caudal peduncle; second ray of the dorsal fin long 25.5-50.7% SL; gill rakers 10-13+22-30 = 33-43.

Description. —Head 17.7-24.7% SL; mouth almost terminal. Snout short, 6.4-7.8% SL. Maxillary with villiform teeth and an external row of canine-like teeth, with three additional rows of relatively small villiform teeth. Dentary with two rows of small canine-like teeth, external ones slightly larger than internal ones. Teeth on vomer canine-like, on a small rounded patch. Barbel on chin very small, occasionally present, 0.4-0.5% SL. Orbit diameter, 4.2-6.3% SL, at least four times in head length. Interorbital wide, 7.5-11.4% SL, more than twice in head length, almost twice in orbit diameter. Maxillary 10.6-13.5% SL., ending at about same vertical as posterior end of orbit. Opercle bone thin, not ending in a spine in its upper portion. Postorbital length 5.7-12.3% SL.

Greatest body depth before area of anus, 13.1-21.7% SL. Depth at first anal fin ray 12.4-19.6% SL. Anus and anal fin separated by distance greater than height of caudal peduncle. Preanus length 25.0-32.2% SL. Preanal fin length 31.1-39.9% SL. Predorsal length 22.1-27.1% SL. Depth at anus 12.0-19.6% SL. Caudal peduncle depth 0.9-1.9% SL.

First dorsal fin with 4-7 rays, base short, 3.2-4.5% SL; first ray embedded in skin, second ray longest, 25.5-50.7% SL, remaining rays gradually decrease in height. Second dorsal fin with 65-77 rays, base long 65.9-74.0% SL, rays gradually decrease in height posteriorly. Anal fin with 60-74 rays, shorter than second dorsal fin 57.0-69.2% SL. Pectoral fin with 18-21 rays, its base 2.7-3.8% SL, prepectoral length 22.9-26.9% SL. Pelvic fin with two elongated rays and two or three smaller rays; length 9.4-27.5% SL, reach extending pass vent to anal fin. Caudal fin asymmetrical, 9-12 lower procurrent rays, upper procurrent rays 7-9, principal rays 5-6. Total vertebrae 55-62, precaudal vertebrae 11-13, caudal vertebrae 44-50. Gill rakers 10-13+22-30, total = 33-43. Lateral line not well defined, with modified scales ca. 20-24, on straight line about 85-105 scales. Scales above lateral line 7-8, below lateral line 15-25.

Comparisons. —The species is characterized by its high number of gill rakers (10-13+22-30) and the long second ray of the first dorsal fin (22.5-50.7% SL). These two characters separate it from all other *Guttigadus*. *Guttigadus globiceps* also differs from *G. globosus* in having fewer pectoral fin rays (18 -21 vs 23-29) and fewer upper and lower procurrent caudal fin rays (7-9 vs 10-12 and 9-12 vs 13-15, respectively); from *G. kongi* in having fewer pectoral fin rays (18-21 vs 22-27) and fewer lateral body scales (85-105 vs 170); from *G. latifrons* fewer scales on a straight line (85-105 vs 145-150); from *G. nudicephalum* in having more second dorsal fin rays (65-77 vs 59-62), fewer pectoral fin rays (18-21 vs 27-28), more caudal vertebrae (44-50 vs 36-38), and fewer scales above and below the lateral line (7 -8 vs 18-20 and 15-25 vs 40-55, respectively).

Color in alcohol. —Body completely light brown to yellowish; all fins whitish; visceral area dark from black peritoneum; anterior area above head bluish, as are areas below orbit and operculum; mouth dark.

Distribution. —*Guttigadus globiceps* is distributed widely on continental slopes in the Southern Ocean. It was described originally by Gilchrist (1906) from off Cape Point, South Africa. Thompson (1916) recorded specimens from off Lota, Chile, and described them as a new species (*Laemonema multiradiatum*). Paulin (1983) included *G. globiceps* in the New Zealand fauna. Markle and Meléndez (1988) redescribed the species from off Chile. It has been captured at depths between 730-1360 m (Fig. 33).

Material examined. —Syntypes-SAM 12488 (4, 117-143), Cape Point E 1/2 N 34 miles. 500 fms. other-AMS I.18712010, ISH 187/67, LACM 44762-1, MNHNC P6439, MNHNC P6440, MNHNC P6566, MSU 16048, MSU 17194, MSU 17201, MSU 17206, MSU 15857, MSU 17195, MSU P17200, MSU P17202, MSU uncat. (South Atlantic), SAM 12445, SAM 12447, SAM 12448, SAM 12450, SAM 12489, SAM 12490, SAM 12491, SAM 12492, SAM 12493, USNM 76858 (holotype of *Laemonema multiradiatum*), USNM 304551, USNM 304558, USNM 304557.

Guttigadus nana (Taki, 1953)
Figure 32d

Laemonema (*Guttigadus*) *nana* Taki,1953:201-210.
Laemonema nana: Okiyama, 1986:321-333 (larval stages). Okamura, 1984:91, Parin, 1984:57. Markle and Meléndez, 1988:875. Cohen et al., 1990 (list).

Diagnosis. —A dwarf species (maximum size 73.1 mm SL) with short, slightly deep body, covered by small, deciduous scales; body ending in a narrow caudal peduncle; upper gill rakers 1-2; interorbital width 5.2-7.1% SL, equal to or shorter than orbit diameter (6.3-7.4% SL); vomer toothless; caudal vertebrae 27-30; anal fin rays 46-53.

Description. —Head 23.3-26.0% SL; mouth subterminal to terminal, slightly inclined. Snout short, 5.6-6.9% SL. Maxillary and dentary with three or more rows of small canine-like teeth. Vomer toothless. Barbel on chin, 4.4-6.4% SL, equal to or smaller than orbit diameter. Orbit small, 6.3-7.4% SL, at least four times in head length. Interorbital narrow 5.2-7.1% SL, almost four times in head length, slightly shorter than orbit diameter. Maxillary 10.9-12.9% SL, ending at about same vertical as end of pupil. Opercle bone border continuous along upper portion. Postorbital length 12.8-14.8% SL. A conspicuous whitish area behind orbit, where swimbladder connected with skin.

Greatest depth of body between anus and insertion of pelvic fin, 15.6-21.1% SL. Depth at anus 15.6-19.8% SL. Depth at first anal ray 16.2-19.8% SL. Anus and anal fin not separated. Preanus length 31.6-42.2% SL. Preanal length 34.7-43.8% SL. Predorsal length 27.7-32.2% SL. Caudal peduncle depth 3.2-4.2% SL.

First dorsal fin with 4-6 rays; short base 5.0-6.6% SL; first ray shortest, third ray longest, 3.5-11.7% SL, longer than caudal depth in well-preserved specimens; remaining rays decrease slightly in height. Second dorsal fin with 45-54 rays; base large, 56.2-62.3% SL; ray height gradually decreases from beginning to end. Anal fin with 46-53 rays, shorter than second dorsal fin 47.0-59.6% SL. Pectoral fin with 22-24 rays, its base 5.2-5.8% SL; prepectoral length 25.6-28.1% SL. Pelvic fin with three rays, exterior two longest, length 15.0-17.2% SL, but not reaching vent. Caudal fin asymmetrical, 9-10 lower procurrent rays, almost equal to or slightly greater than upper procurrent rays, 7-8, principal rays 6 (one specimen with 5 rays). Total vertebrae 39-41, precaudal vertebrae 10-12, caudal vertebrae 27-30. Gill rakers 2-1+6-4, total = 5-8. Lateral line with 60-75 scales on an straight line. Scales above lateral line 8.

Comparisons. —*Guttigadus nana* is the smallest (42.3-73.1 mm SL) and shallowest-living member of the *Laemonema-Guttigadus* group. It also has the lowest number of rays in the second dorsal and anal fins, and lowest number of caudal vertebrae (27-30). It shares small size and low meristics with the other paedomorph, *L. verecundum*.

Color in alcohol. —Body light brown, fins almost transparent. A white semi-circle in upper operculum area, where anterior part or cornua of swimbladder connected to skin.

Distribution. —Only known from epipelagic waters off Japan (Fig. 33) in very shallow depths (25-60 m).

Comments. —Taki (1953) erected a subgenus *Guttigadus* based on its small size, presence of sensory papillae on lateral line, reduced gill rakers, low number of rays in second dorsal and anal fins, and low number of vertebrae. The material we examined included sexually mature females, which suggests that *G. nana* is paedomorphic. The process of paedomorphosis in this species appears to involve mostly reductions in serially repeating structures, including vertebrae, vertical fin rays procurrent caudal rays, and gill rakers in the upper arch (Table 4). A similar reduction in serial structures is also seen in the other paedomorph, *L. verecundum*. *Guttigadus nana* has lost pharyngobranchials 1 and 2 (Fig. 5a) which might also reflect a reductionist developmental program and suggest that pharyngobranchial 2 might be a late-forming element. In addition, there are several loss character states correlated with the loss of pharyngobranchial 1: absence of the uncinate process, interarcual ligament, and interarcual cartilage (Fig. 5a). Absence of the vomer and the neck on the swimbladder (Fig. 7e) might also reflect reductionism, as does the absence of a laminar bone on the first pterygiophore of the first dorsal fin (Fig. 14c).

Two larvae (4.1 and 11.3 mm SL) were described by Okiyama (1986). The largest specimen had developed all fin rays whereas the smallest had not. A series of sensory pits on the opercle were also developed on the largest specimen. Both were lightly pigmented; a vertically barred juvenile stage has not been described.

Material examined. —BSKU 42415, BSKU 42416, UMMZ 212836, UMMZ 214587, UMMZ 214588, USNM 273285.

Guttigadus globosus (Paulin, 1985)
Figure 35

Momonatira globosus Paulin, 1985: 357.
Momonatira globosus: Markle and Meléndez, 1988:875. Trunov, 1989:179-185. Cohen et al., 1990:368.
Momonatira paulini Trunov, 1989:179-185.
Momonatira paulini: Cohen et al, 1990:368.

Diagnosis. —Body deep; head large; caudal peduncle narrow; lower jaws included (overlapped by) upper jaws when mouth closed; interorbital very wide, 10.3-15.0% SL; barbel on chin very short, 0.3-1.0% SL; lining of mouth dark.

Description. —Head length 22.4-28.6% SL; scales lacking on head. Maxillary 8.8-12.5% SL, its end reaching end of pupil; two or three rows of short caniniform teeth, plus one or two inner rows of small villiform teeth, that do not reach end of upper jaws. Dentary with one row of short, strong, caniniform teeth and a short row of inner teeth. Lower jaws included. Small, rounded vomer with teeth. Snout short, 6.7-10.0% SL, larger than orbit diameter. Orbit diameter 4.5-7.5% SL, smaller than interorbital width, 10.3-15.0% SL. Barbel on chin very short 0.4-1.0% SL. Postorbital length 11.0-14.4% SL.

Predorsal length 25.3-34.8% SL. Anus completely separated from anal fin, preanal length 30.6-42.6% SL, preanus length 28.3-32.9% SL. Pectoral fin inserted just before origin of first dorsal fin; prepectoral length 24.9-28.6% SL. Pelvic fins well before insertion of pectoral and first dorsal fins; prepelvic length 17.5-22.3% SL. Body at first anal ray 13.2-20.3% SL.

Figure 35. *Guttigadus globosus*, NMNZ 15861, 181 mm SL.

First dorsal fin with 5-6 rays, very short, height 4.5-10.6% SL. Second dorsal fin with 70-83 rays, its base 63.1-77.3% SL; last rays of second dorsal and anal fin ending almost at same vertical. Anal fin with 73-84 rays, its base 59.9-70.2% SL. Pectoral fin with 23-29 rays, its base 3.8-5.1% SL, its length 6.4-14.3% SL. Pelvic fins with two long and three shorter rays, longest rays 4.0-13.9% SL. Caudal fin asymmetrical, upper procurrent ray 10-12, principal rays 6, lower procurrent rays 13-14. Total vertebrae 56-59, precaudal vertebrae 12-14, caudal vertebrae 42-47. Gill rakers 6-8+17-20, total = 23-28. Modified scales on lateral line ca. 16-25. Scales on a straight line 111 -137, scales above lateral line 12, scales below lateral line 27.

Comparisons. —*Guttigadus globosus* differs from *G. kongi* in having more total vertebrae (56-59 vs 49-56), fewer lateral body scales (111-137 vs 170), a longer anal fin base (59.9-70.2 vs 52.1-59.9), lower jaws included, and a pigmented rather than an unpigmented lining of the mouth. *Guttigadus globosus* appears to live deeper (1175-1600 m) than *G. kongi* (83-1500 m). *Guttigadus globosus* differs from *G. latifrons* in having more lower limb gill rakers (17-20 vs 14-17), fewer scales below the lateral line (27 vs 38), a broader interorbital (10.4-14.8 vs 7.7-10.4% SL), shorter barbel (0.3-1.0 vs 1.9-3.9% SL), and inclusion of the lower jaws in the upper jaws. *Guttigadus globosus* differs from *G. nudicephalum* in having more second dorsal fin rays (70-83 vs 59-62), more anal fin rays (73-84 vs 56-60), more caudal vertebrae (42-47 vs 36-38), and more upper and lower gill rakers (6-8 vs 3-5 and 17-22 vs 10-11, respectively).

Color in alcohol. —Body yellowish, visceral area dark brown. All fins have dark membranes. Head mostly whitish, except snout, below orbit, around mouth, and on dentary. Interior of mouth dark blue, gill chambers dark.

Distribution. —*Guttigadus globosus* is known from oceanic islands at depths of 1200-1500 m off New Zealand (Paulin 1985), and 1175-1600 m in the mid South Atlantic (Trunov, 1989; Cohen et al., 1990) (Fig. 34).

Figure 36. *Guttigadus nudicephalum*, PPSIO uncat, 82 mm SL.

Comments. —*Guttigadus paulini* Trunov, 1989 is considered a synonym because of the overlap in all morphometric and meristic values. Some meristic counts suggest slight geographic or population differences (Table 7), but we found no substantive diagnostic differences. The best diagnostic character, according to the literature, is the number of pyloric caeca: Paulin (1985) reports 3-4 for *G. globosus* and Trunov (1989) reports 10-11 for *G. paulini*. However, a paratype of *G. globosus* (NMNZ 15861) has 10 pyloric caeca, suggesting the need to re-evaluate Paulin's counts. In a related matter, Paulin (1985) reported high pectoral fin rays counts of 28-30 for *G. globosus*, but our counts in two paratypes (NMNZ 15828 and 15863) were 25 and 26, respectively.

Material examined. —NMNZ P15828 (paratype), NMNZ P15861 (paratype), NMNZ P15863, NMNZ P25203, MSU 16054, MSU 16053, MSU 13720, MSU uncat. (41° 59'S, 00° 25'E, 12 XII 1979).

Guttigadus nudicephalum (Trunov, 1990)
Figure 36

Paralaemonema nudicephalum Trunov, 1990:81-83.

Diagnosis. —Body short, ending in narrow caudal peduncle; head large scaleless; gill rakers 3-5+10-11; vomer triangular; modified scales on lateral line ca. 14-15.

Description. —Head length 27.3-31.1% SL. Mouth subterminal, maxillary 13.0-15.0% SL, one outer row of strong caniniform teeth and one inner row of small teeth that does not continue to end of maxillary. Dentary with teeth pattern similar to that in maxillary. Vomer triangular, with small teeth. Barbel on chin 3.5-4.2% SL. Orbit diameter 7.5-9.5% SL, smaller than interorbital width, 8.9-11.3% SL. Postorbital length 14.8-16.7% SL.

Predorsal length 30.5-33.6% SL. Anus separated from anal fin; preanus length 40.3-47.5% SL; preanal length 43.0-51.0% SL. Pectoral fin insertion behind insertion of first dorsal fin; prepectoral length 32.3-34.3% SL. Prepelvic length 27.1-31.9% SL.

Meristic characters in parentheses are from Trunov's (1990) holotype. First dorsal fin with 4-5(4) rays, second ray longest 6.1-8.5% SL. Second dorsal fin with 59-62(66) rays, its base 58.3-60.6% SL. Anal fin with 56-60(61) rays, its base 51.7-55.0% SL, last rays almost reaching last rays of second dorsal fin. Pectoral fin with 27-28(26) rays, its base 7.1-8.8% SL, its length 15.8-20.5% SL. Pelvic fin with two large and two shorter rays, its length 23.8-29.1% SL. Total vertebrae 48-51, precaudal vertebrae 12-13, caudal vertebrae 36-38. Caudal fin slightly asymmetrical, upper procurrent rays 11-12, principal rays 6, lower procurrent rays 12-14. Gill rakers 3-5(4)+10-11(10), total = 13-15(14). Modified scales on lateral line 14-15; lateral body scales about 114-135(140). Scales above lateral line 18-20(18), scales below 40-55.

Comparisons. —*Guttigadus nudicephalum* differs from other *Guttigadus* in its low dorsal fin ray and vertebral counts (Table 4), being higher than *G. nana* but lower than all others.

Color in alcohol. —Body light yellow to yellowish, visceral area gray; all fins dark, most of head brown, except in area of branchiostegal membranes; a conspicuous brown spot between pelvic fins.

Distribution. —This species is known only from the Indian Ocean from 24° 54'S, 61° 25'E (Whale Ridge) to 25° 09'S, 35° 36'E (Fig. 45), at depths of 630-1000 m.

Material examined. —MSU uncat. (R/V VITYAZ, Indian Ocean), PPSIO uncat. (25° 09'S, 35° 36'E, 24-25 XI 1988).

Species *incertae sedis*

Guttigadus nudirostre (Trunov, 1990)
Paralaemonema nudirostre Trunov, 1990:81-83.
Paralaemonema nudirostretira, (*lapsus*), Trunov, 1990:81-83.

Description. —(from original paper) D1 4- 6, predominantly 5; D2 63-74; A 63-70; P1 24-25, most often 25; P2 4-5, very rarely 5; gill rakers 6-7+13-18, scales on lateral line 21-25; scales on a transverse series 120-140; pyloric caeca 7-11; total vertebrae 12+41. Predorsal length 28.8-32.0% SL; preanal length 42.4-47.0% SL, maxillary 12.2-14.8; orbit diameter 6.9-8.3% SL; interorbital length 10.1-11.6% SL. Base color of body cinnamon brown with brownish tinge. Walls of anterior mouth and gill cavities, gill filaments, and pyloric caeca light, inner region of mouth and gill cavities (toward throat and bases of gill arches) darkish blue.

Holotype: ZIN 48159 (189), 42° 05'S, 1° 21'E, 800 m, 3 April 1981. Paratypes: ZIN 48159 (3, 167-183), same data as holotype. ZIN 48160 (2, 147-203), 42° 03'S, 0° 11'E, 550-580 m, 28 July 1976. ZIN 48161 (2, 147-158), 41° 52'S, 0° 18'E, 500-525 m, 29 July 1976.

Distribution. —The species is known only from the Discovery Seamount, where it was collected at depth of 500-800 m.

Comments. —This species is similar to *G. kongi* and *G. latifrons*, and shares the light mouth pigmentation and the bathymetric range of *G. kongi*. According to the original description of *G. nudirostre*, it has fewer lateral body scales (120-140) than

G. kongi (ca. 170). We treat this species as incertae sedis, suspecting it to be a junior synonym of *G. kongi*.

Guttigadus squamirostre (Trunov, 1990)

Paralaemonema squamirostre Trunov, 1990:81-83.

Description. —(from original paper) D1 4; D2 64; P1 24; P2 5; gill rakers 8+16, scales above lateral line about 26; transverse series about 160. Predorsal length 27.1% SL; preanal length 37.3% SL, orbit diameter 8.2% SL; interorbital width 8.8% SL. Body brownish cinnamon. Mouth and gill cavities (apart from darkish blue region around throat and near bases of gill arches), gill arches and rakers light cinnamon brown.

Holotype: ZIN 48157 (161), 31° 20'S, 15° 51'E, 517 m, 24 August 1976.

Distribution. —Off the southwestern coast of Africa at a depth of 517 m.

Comments. —This species is also similar to *G. kongi* and *G. latifrons*, and again shares the light mouth pigmentation and bathymetric range of *G. kongi*. Trunov reports approximately 23 scales above the lateral line in *G. squamirostre*, almost double our counts in *G. kongi* (12). This difference in squamation suggests the existence of another species.

Laemonemodes compressicauda Gilchrist, 1903

Laemonemodes compressicauda Gilchrist, 1903:208-209.

Laemonemodes was established for those *Laemonema* having pelvic fins with two long rays plus six minute rays. This is an important characteristic because of the ontogenetic reduction in number of inner pelvic rays documented for juvenile *L. barbatulum* (Fig. 23; Fahay and Markle, 1984). Norman (1966) synonymized *Laemonemodes* with *Laemonema* by amending the generic diagnosis as follows: "...with or without some minute inner rays in pelvic fin."

Laemonemodes compressicauda Gilchrist (1903) was based on an approximately 60 mm SL individual from the east coast of South Africa which may have been loaned to the British Museum, but which is apparently lost (P. A. Hulley, South African Museum, pers. comm., 23 June 1988; J. Chambers, British Museum Natural History, pers. comm., 16 October 1989). Unfortunately, the reported low second dorsal fin (46) and anal fin ray (46) counts most closely resemble *G. nana*. It seems unlikely that the shallow-living *G. nana* from Japan is conspecific with the deep-living (550-735 m) *L. compressicauda* from South Africa. A reported second specimen (Cohen 1986) may be the specimen we designate as the holotype of *L. macronema*. Although from the same general area as *L. compressicauda*, *L. macronema*'s dorsal (57-58) and anal (54-55) fin ray counts are at least 11 (dorsal) or 8 (anal) rays higher. The largest range we document in *Laemonema* is in *L. laureysi* where the range is 10 for anal and 9 for dorsal rays (Table 4). We treat *L. compressicauda* as *incerta sedis*.

Zoogeography

The zoogeography of the two genera are fundamentally different. Howes (1990) pointed out that gadoids, including morids, have a marginal oceanic distribution, following conti-

nental margins or sea mountain chains. *Laemonema* has a worldwide distribution, except for the northeastern Pacific Ocean and possibly the eastern Indian Ocean. It occurs from 60° N to 40° S, is most abundant at approximately 200-600 m depth and reaches its greatest diversity in the Pacific (Figs. 24, 25, 34). *Guttigadus* is most diverse between 25° S-59° S, in the Southern Hemisphere, with one species extending into the eastern North Atlantic, *G. latifrons*, and one western North Pacific endemic, *G. nana* (Fig. 34). Most species of *Guttigadus* live deeper than *Laemonema*, being most abundant at approximately 600-1600 m. As in many genera, *Laemonema*'s zoogeography is dominated by the influence of anti-cyclonic gyres in the Atlantic, Pacific and Indian oceans, while *Guttigadus*'s is dominated by the circumpolar circulation of the Southern Ocean (Lutjeharms, 1990).

Resolved species pairs in *Laemonema* (Fig. 18) are allopatric: in the Atlantic Ocean, *Laemonema barbatulum* plus *L. yarrelli*, and in the North Pacific, *L. longipes* plus *L. verecundum* (Figs. 24, 25). One pair, *L. robustum* and *L. macronema*, might be allopatric but their distributions are unclear. All pairs show east-west segregation. The Pacific sister species, *L. longipes* and *L. verecundum*, also exhibit a latitudinal difference, with *L. longipes* in the temperate western North Pacific and *L. verecundum* in the tropical eastern Pacific (Fig. 24).

Species of *Laemonema* associated with oceanic islands, trenches and seamounts do not appear to form a clade, nor are they consistently sister taxa to continental forms. However, in two resolved clades, an oceanic form is sister to a continental form or clade (*L. verecundum* with *L. longipes* and *L. yarrelli* with *L. barbatulum*, Figs. 18, 24). Vicariant events are not clear within *Laemonema*. A North Pacific species pair, *L. longipes* and *L. verecundum*, are largely allopatric with the rest of the genus and could have come from an early event that separated them from a widely distributed tropical ancestor (Fig. 24), much as we imagine the *Guttigadus* scenario below. Resolution of the problematic *L. robustum* distribution pattern might provide some insight regarding the *L. melanurum* terminal clade (Fig. 25). *Laemonema robustum* and *L. rhodochir* have the broadest latitudinal and longitudinal distribution in the genus (Figs. 24, 25). The distribution of *L. robustum* in the Pacific and Atlantic Ocean is difficult to analyze because there are few samples. With larger samples, we find no differentiation of populations in *L. rhodochir* in the Pacific Ocean. Widely distributed morids have been documented in other taxa with larger data sets, such as *Antimora rostrata* (Small, 1981) and *Halargyreus johnsoni* (Cohen et al., 1990), the latter of which has a distribution similar to *L. robustum*.

Guttigadus (Fig. 18) seems to have originated and evolved, mostly, in the Southern Ocean, north of the Antarctic Convergence. Miller (1993) mentions a secondary Antarctic fish fauna of midwater and near-bottom fishes belonging to World Ocean families. *Guttigadus* is clearly part of this fauna. Its diversity and subsequent dispersal into the northern hemisphere is some indication of the age of this fauna.

The distribution of several *Guttigadus* species supports Anderson's (1990) contention that many poorly known deeper living benthic species have a circumpolar distribution. However, two early vicariant events in the clade were the isolation of *G. nana* and *G. latifrons* in the Northern Hemisphere (Fig. 34). The first event, the speciation of *G. nana* (Fig. 18), involved a bathymetric change as well as latitudinal isolation. In other members of *Laemonema* sensu lato, the shallowest bathymetric stage is the pelagic juvenile stage which is found in surface layers (Markle 1989). The paedomorphic morphology of *G. nana* (see above) is consistent with neotenic retention of the shallow water juvenile

habitat. The evidence indicates that this earliest vicariant event in *Guttigadus* involved accelerated gonadal development in a juvenile stage (neoteny) and resulted in a unique endemic off Japan (Fig. 34).

The other latitudinal vicariant event involved the dispersal and isolation in the North Atlantic of *G. latifrons* (Figs. 18, 33) from a widely distributed Southern Ocean ancestor of *G. globosus*, *G. kongi*, and *G. nudicephalum*. Its South African populations presumably represent a recent re-invasion of the Southern Ocean.

Three of the remaining five *Guttigadus* are mostly found deeper than 1000 m with *G. nudicephalum* and *G. kongi* being generally shoaler. Vicariance along a bathymetric gradient would be the simplest explanation of the speciation events (Fig. 18). The most interesting of these is the event which produced the sympatric sister taxa, *G. kongi* and *G. globosus* (Fig. 33). The shoaler-living *G. kongi* has a total depth range of 83-1500m, being most abundant from about 500-800 m over its geographic range (Markle and Meléndez 1988). The deeper-dwelling *G. globosus* (1175-1600 m) presumably retains the ancestral depth pattern. The circumpolar, or nearly circumpolar, distribution of *G. kongi*, *G. globiceps* and *G. globosus* is also seen in other outer slope fishes of the Southern Ocean (Anderson 1990, Gon and Heemstra 1990). *Guttigadus nudicephalum* could also represent peripheral bathymetric speciation of a shallow Indian Ocean endemic from the ancestral Southern Ocean stock. It is known only from the southern tip of South Africa (Fig. 34).

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